ABSTRACT

Title of Document:MAPPING QUANTITATIVE TRAIT LOCI
FOR GRAIN YIELD AND YIELD RELATED
TRAITS IN A HEXAPLOID WINTER WHEAT
DOUBLED HAPLOID POPULATION

Yaopeng Zhou, Doctor of Philosophy, 2015

Directed By:

Dr. José M. Costa, Professor Emeritus Department of Plant Science and Landscape Architecture

Improving wheat grain yield potential is imperative to match the increasing food demand associated with a fast growing population. Genetic and modeling approaches were employed to investigate the genetic basis and phenotype network regarding grain yield and yield related traits in a soft red winter wheat doubled haploid population. The population and two parents were evaluated in five year-location trials in the USA and genotyped by high throughput DNA markers including simple sequence repeat (SSR) and single nucleotide polymorphism (SNP). Bi-parental linkage mapping identified a number of QTLs for grain yield and yield related traits among which sixty were for grain yield components (GYLD, grain yield; SPSM, spikes per square meter; TGW, thousand grain weight; GPS, grains per spike; GWPS, grain weight per spike), seventy four were for plant architecture (PHT, plant height; FLL, flag leaf length; FLW, flag leaf width; FLA, flag leaf area; FLS, flag leaf shape

or length/width ratio), and one hundred and nine were for spike morphology (SL, spike length; TSN, total spikelet number per spike; FSN, fertile spikelet number per spike; SSN, sterile spikelet number per spike; SC, spike compactness; GSP, grains per spikelet). In addition, structural equation modeling is described to construct a phenotype network. It revealed that GSP and FSN may mediate yield component compensation. Furthermore, doubled haploid lines DH96 and DH84 may have potential as new high-yielding cultivars for the Mid-Atlantic region.

MAPPING QUANTITATIVE TRAIT LOCI FOR GRAIN YIELD AND YIELD RELATED TRAITS IN A HEXAPLOID WINTER WHEAT DOUBLED HAPLOID POPULATION

By

Yaopeng Zhou

Dissertation submitted to the Faculty of the Graduate School of the University of Maryland, College Park, in partial fulfillment of the requirements for the degree of Doctor of Philosophy 2015

Advisory Committee: Professor Dr. José M. Costa, Chair Professor Dr. James N. Culver Professor Dr. Shunyuan Xiao Professor Dr. Zhongchi Liu Special Member Dr. Qijian Song © Copyright by Yaopeng Zhou 2015

Dedication

I would like to dedicate this dissertation to my parents, Xueyi Zhou and Yuyun Hu,

for their unconditional and endless love through my whole life and to my brother,

Yaodi Zhou, for inspiring and supporting me along the way.

Acknowledgements

I would like to acknowledge my advisor, Dr. José M. Costa, for leading me down to the path of plant breeding and genetics and his continuing support throughout my study at the University of Maryland. Thanks also to my other committee members: Dr. Zhongchi Liu, Dr. James N. Culver, Dr. Shunyuan Xiao, and Dr. Qijian Song for their constructive suggestions, guidance, and encouragement. I would also like to thank the farm crew at the Wye Research & Education Center and the Central Maryland Research & Education Center for their aid in fungicide and fertilizer application. Particularly, I want to thank Aaron Cooper for his help from planting to harvesting. I would not have been able to complete my work without the support from my collaborators from USDA-ARS: Dr. Shiaoman Chao, Dr. Gina Brown-Guedira, and Dr. David Marshall who made great contributions in the genotyping and field evaluation and Dr. Paul Murphy from the North Carolina State University, who produced the doubled haploid mapping population. I also want to thank my lab mates, Ben Conway and Daniela Miller, for their invaluable discussions and the happy hours we spent together at the Looney's Pub. My graduate school experience would be totally different without them. Thanks also to my friends at the Grad Office 2125: Siqi Chen, Justine Beaulieu, Sara Allard, Chioma Egekwu, and Laura Templeton who encouraged and listened to me during my hardest time.

Participants contribution

The project was initiated and guided by Dr. Jose Costa. The doubled haploid population was produced by Dr. Paul Murphy from North Carolina State University. 9K SNP array was conducted by Dr. Shiaoman Chao from USDA-ARS Small Grains Genotyping Lab at Fargo, ND. Dr. Gina Brown-Guedira from USDA-ARS Eastern Regional Small Grain Genotyping Lab at Raleigh, NC prepared the DNA library and sent it to USDA-ARS Central Small Grain Genotyping Lab at Manhattan, KS for genotyping-for-sequencing. All genotype calls were made by Dr. Gina Brown-Guedira. I performed maker quality assessment, constructed the linkage map, proposed and finished phenotype network modeling. I also performed the QTL mapping/analyses, phenotypic data analyses and wrote the manuscript. The manuscript consists of five independent prepublication chapters.

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List of Abbreviations

FLA	Flag leaf area, cm ²
FLL	Flag leaf length, cm
FLS	Flag leaf shape
FLW	Flag leaf width, cm
FSN	Fertile spikelet number per spike
GPS	Grains per spike
GSP	Grain number per spikelet
GWPS	Grain weight per spike, g
GYLD	Grain yield, g m ⁻²
HD	Heading date, days
PHT	Plant height, cm
QTL	Quantitative trait locus
SC	Spike compactness
SL	Spike length, cm
SPSM	Spikes per square meter
SSN	Sterile spikelet number per spike
TGW	Thousand-grain weight, g
LOD	Logarithm of the odds
PVE	Phenotypic variation explained, percentage
SSR	Simple sequence repeat
SNP	Single nucleotide polymorphism
SEM	Structural equation modeling

Chapter 1: Literature review

Introduction

Improving grain production is the key to ensuring food supply and social stability across the globe. In the last century, the great success of Green Revolution featuring highyielding dwarf rice and wheat plants under heavy nitrogen fertilizers helped to feed an increasing population. However, it has come to a point where continuous yield increases driven by successful breeding management might be approaching a ceiling. This review aims to provide the most current developments in wheat grain yield improvement by examining the yield and yield contributing traits from a physiological and genetic perspective and by describing state-of-art technologies in current breeding practice.

Increasing population and food supply

According to the official estimates and projections from United Nations, the world population will reach 8.1 billion in 2025, and further increase to 9.6 billion in 2050 and 10.9 billion by 2100 (UN DESA, 2013). Meanwhile, global crop production needs to double by 2050 to meet the demands from the rising population, changing diets, and increasing biofuel consumption (FAO, 2012; Tilman et al., 2011). Yields of major crops like maize, rice, wheat, and soybean, however, are increasing at only 1.6%, 1.0% 0.9% and 1.3% per year, which is far slower than the 2.4% per year rate required to double global production by 2050 (Ray et al., 2013). Yield potential improvement is critical to meet this challenge.

Wheat evolution

The allohexaploid bread wheat (*Triticum aestivum* L.; 2n = 6x = 42 chromosomes; genomic code AABBDD) is the product of two hybridization events involving three diploid (2x; 2n = 14) grass species within the tribe Triticeae: *Triticum urartu* (AA), an unknown close relative of *Aegilops speltoides* (BB), and *Aegilops tauschii* (DD) (Marcussen et al., 2014). The first hybridization is hypothesized to happen between the A and B genome donors 300,000–500,000 years ago, resulting in the wild tetraploid emmer wheat (*Triticum turgidum*; AABB) (Marcussen et al., 2014; Peng et al., 2011). About 10,000 years ago, emmer wheat cultivation began and expanded eastwards from the Fertile Crescent to the natural habitat of wild grass *Aegilops tauschii* during which cultivated emmer wheat hybridized with this D genome donor to form modern hexaploid bread wheat (AABBDD) (Peng et al., 2011; Shewry, 2009).

Brief overview of quantitative genetics

Phenotype classification

Phenotype or the expression of a trait is an observable characteristic of an individual and varies between individuals. Phenotypes of organisms are classified into three different forms: qualitative, quantitative and threshold traits (Birnbaum, 1972). A qualitative trait is expressed discretely and individual phenotypes fall into discrete categories, as opposed to a quantitative trait, where phenotypes show a continuous range of values such as weight and height (Abiola et al., 2003). Threshold traits are dimorphic traits with polygenic bases but show a limited number of phenotypes such as molting in insects which is controlled by the levels of juvenile hormones (Moorad and Linksvayer, 2008;

Roff, 2008). In agricultural production, most agronomic traits of economic importance are quantitative traits.

Genetic and environment values

Quantitative traits have been extensively studied since the 1920s, after the establishment of quantitative genetics, which, in conjunction with statistics and Mendelian genetics, provided the scientific framework for modern plant breeding (Lamkey and Lee, 1993). Usually, quantitative traits show phenotypic variation among individuals and have a complicated genetic architecture, involving many genes throughout the genome with variable contributions to the overall phenotype (Holland, 2007). The genes controlling quantitative traits are affected by gene-by-gene and gene-by-environment interactions (Xu and Zhu, 2012). The environment, defined as the integrated influence of all nongenetic variables affecting phenotype, adds more complexity to quantitative traits (Xu and Zhu, 2012).

One of the fundamental principles of quantitative genetics is that the phenotypic value P of an individual for a given trait can be considered as the sum of that individual's genotypic value G plus the environmental value E, thus, in linear format: P=G+E, where G can be divided into additive (A), dominant (D) and epistatic (I) values (Walsh, 2001). To better account for quantitative traits, especially in breeding, the additive model needs to be extended to include $G \times E$, which is known as genotype-by-environment interaction (Eeuwijk, 2008). In natural populations, the variation of a quantitative trait often approximates a statistical normal distribution as it is the sum of small effects caused by genes and the environment (Xu, 2010). Most important agronomic traits that constitute

the primary focus of plant breeding such as grain yield are quantitative in nature, usually referred to as complex traits, with variation believed to be attributable to dozens if not hundreds of underlying genes (Crosbie et al., 2008). A region of the genome containing one or more genes that affect variation in a quantitative trait is known as quantitative trait locus (QTL). QTL identification and diagnostic marker development for desired traits are crucial so that modern breeders can deliver superior new cultivars with efficiency and accuracy.

<u>Yield-related quantitative traits in wheat</u>

Grain yield

Improving the grain yield potential of wheat has been the principal aim of wheat breeding programs worldwide and has helped to maintain the viability of agricultural systems in both developed and developing countries (Kuchel et al., 2007b). Although, genetic improvement in yield potential, resistance to diseases, and adaptation to abiotic stresses have contributed to the increases of grain production in the last three decades, it is widely accepted that the rates of progress and genetic gains from wheat breeding have slowed down and even decreased (Reynolds et al., 2012; Reynolds et al., 2009). Part of the reason is due to the lack of sufficient knowledge about the mechanisms, complex biological pathways, and their corresponding genetic basis underlying the responses of wheat in specific environments (Henry and Prasanta, 2004). In recent years, the rapid advances in biotechnology and molecular biology, as well as research on model organisms, have provided powerful tools and references for crop genetic improvement.

Our current understanding of grain yield and its genetic constraints can be expressed by the following three perspectives:

- 1) The classical view: Grain yield = Spikes/ $m^2 \times$ Grains/spike \times Grain Weight;
- The carbon-economy-based view: Grain yield= Light intercepted (LI) × Radiation use efficiency (RUE) × Harvest index (HI);
- The water-use-based view: Grain yield= W × Water use efficiency (WUE) × Harvest Index (HI);

where RUE is the overall photosynthetic efficiency of the crop; W is the water transpired by the crop plus direct evaporation from the soil; WUE is the ability of the crop to produce biomass per unit of water evapotranspired (Matthew et al., 2004).

A new strategy to boost wheat productivity through genetic intervention has been proposed, combining these three views. It features higher photosynthetic capacity, improved partitioning of assimilates and genetic tools to improve breeding efficiency (Reynolds et al., 2012).

Grain yield is the end product of the interaction of a large number of physiological and biochemical processes, genetically complex, and determined concurrently by multiple plant characteristics (Marza et al., 2006; Sharma et al., 2003). The conventional method to explore complex traits is to deconstruct them into simpler components for further exploration and characterization. In the case of wheat grain yield, these include grains per spike, spikes per unit area and grain weight (1000-grain-weight) (Mengistu et al., 2012). Breeding efforts focused on partitioning more assimilates to reproductive development and less to vegetative dry matter production have resulted in modern wheat cultivars with more grains per spike and more grains per square meter (Frederick and Bauer, 1999). Wheat genetics studies have located QTLs for grain yield and yield components on all 21 chromosomes of bread wheat (Bennett et al., 2012a; Heidari et al., 2011; Wu et al., 2012). However, the quantitative nature of QTLs and their strong interaction with the environment make constant and stable QTL detection difficult and their applicability limited to a very specific environment even though a number of them are major QTLs accounting for more than 10% of the phenotypic variation, as was verified by Heidari et al. (2011). Furthermore, the unstable correlation between grain yield and yield components reported from separate studies indicates its underlying complexity (Bennett et al., 2012a; Heidari et al., 2011; Mengistu et al., 2012). Availability of large sets of phenotypic data, genomic data from SNP arrays and new QTL mapping methods will help to detect more QTLs and elucidate the relationships between grain yield and its related traits with more precision.

Plant architecture

Canopy architecture of higher plants is defined by the degree of branching, internodal elongation, and shoot determinacy or, simply, as the spatial configuration of the aboveground plant organs (Fageria et al., 2006; Wang and Li, 2008). Some of the detailed characteristics of plant architecture involve plant height, tillering, branching patterns, leaf size and shape, configuration of leaf relative to the sun and spatial arrangement of leaves (Fageria et al., 2006). Plant architecture has been a focus of research because of its close association with photosynthesis and grain yield (Hedden, 2003).

Plant height, mainly determined by stem elongation, is an important agronomic trait in cereal crops influencing plant architecture and contributing to grain yield (Wang and Li, 2008; Wang et al., 2010). In high soil fertility conditions, the stems of tall cultivars are unable to support the resultant weight of plump grains. High-yielding cultivars fall over in the field before maturity, a process known as lodging, with consequent large yield losses (Hedden, 2003). Introduction of dwarfing genes into cereal crops, such as *Rht-B1b* and *Rht-D1b* in wheat and *sd1* in rice, produced semi-dwarf plants with short strong stalks as well as more assimilate partitioned into the grain leading to the great increases of wheat and rice yield, known as the Green Revolution (Hedden, 2003). Since then, the semi-dwarf phenotype has been extensively selected as the ideal trait for high-yielding cultivars in modern crop breeding programs. However, extremely short plants are disadvantageous because leaves are very closely spaced on a short stem causing increased shading within the canopy, as well as poor ventilation and light transmission in the lower canopy, which affects seed-filling and ultimately decreases yield (Yoshida, 1972; Zhang et al., 2011). Thus, breeding a cultivar with optimum plant height for a target environment is necessary. As with grain yield, QTLs for plant height have been mapped on all 21 chromosomes of wheat (Wu et al., 2010).

Leaves are responsible for photosynthesis that provides photosynthetic products in plants. The flag leaf is the last leaf to emerge before the spike and plays a dominant role in determining grain yield (Yoshida, 1972). Translocation of carbohydrates from the flag leaf is almost entirely directed towards the grain while that from the second and third leaves is only partly directed towards the grain which underscores the important influence of shape and size of flag leaves on yield performance (Monyo and Whittington, 1973). Both Dere and YIildirim (2006) and Monyo and Whittington (1973) found a positive correlation between the flag leaf length and width with grain yield in bread wheat. Among the few QTL studies on leaf morphology in wheat, Jia et al. (2013a) reported a major QTL explaining 28.7-35.6% of the phenotypic variation of flag leaf width and that the Wangshuibai allele reduced flag leaf width up to 3 mm. This QTL was inherited as a semi-dominant gene, designated as *TaFLW1*, and was fine-mapped to a 0.2 cM interval on chromosome 5A (Xue et al., 2013).

Spike morphology

The morphology of wheat spike is characterized by its spike length, fertile spikelet number per spike, sterile spikelet number per spike, and spikelet compactness. The wheat spike harbors spikelets where florets develop and produce grains. Spike morphology is relevant to grain yield because it determines the number of grains. Since the 1960s, genetic gains in grain yield of wheat have generally been achieved by improvements in grain number per spike and spikes per square meter, with little change in individual grain weight (Gaju et al., 2009). Thus, increasing grain number *per se* by modifying the spike morphology may open new opportunities for higher grain yield potential.

In bread wheat, Q, C, and SI are the three major domestication genes affect the gross morphology of the spike. The Q gene is located on chromosome arm 5AL and pleiotropically influences not only spike length and shape, but also other domestication related traits including seed threshability, glume keeledness, rachis fragility, plant height, and spike emergence time (Faris et al., 2014). The C gene is located on chromosome 2D and defines a subspecies of hexaploid wheat known as T. aestivum ssp. compactum (Host) MacKey, or club wheat, which has a characteristic compact spike due to a dominant C allele (Faris et al., 2014). The S1 gene on chromosome 3D defines another subspecies known as T. aestivum ssp. sphaerococcum (Percival) MacKey, or shot wheat, which is characterized by having round seed, round glumes, and a short dense spike (Faris et al., 2014; McIntosh et al., 2013). Therefore, common wheat (ssp. *aestivum*) has the genotype QcS1, club wheat (ssp. compactum) is QCS1, and shot wheat (ssp. sphaerococcum) is Qcs1 (McIntosh et al., 2013). In addition to these loci, all twenty one wheat chromosomes have been associated with spike related traits (Borner et al., 2002; Cui et al., 2012; Deng et al., 2011; Kumar et al., 2007; Ma et al., 2007b; Marza et al., 2006; Wang et al., 2011). Furthermore, mapping QTL as Mendelian factors was first reported by Deng et al. (2011) who investigated wheat spike traits in a F_2 population. This population showed a clear 3:1 segregation ratio for spike number per plant, spike length, and grain number per spike. The underlying QTL was mapped to the chromosome 4B and explained 30.1 to 67.6% of the phenotypic variation across environments. Further fine mapping and molecular characterization of this region has not been reported yet.

<u>Cloned QTL/genes related to grain yield in cereal crops</u>

Grain related traits

Grain morphology and grain filling rate determine grain weight and thus, grain yield. The first cloned major QTL related to grain morphology was GS3 which explained 80-90% of the variation for grain weight and length in a rice BC₃F₂ population derived from a cross between Minghui 63 (large grain) and Chuan 7 (small grain) (Fan et al., 2006). Initial QTL analysis mapped *GS3* on chromosome 3. Fine mapping narrowed down the

candidate region to a DNA fragment of 7.9 kb in length where a full-length cDNA was identified. *GS3* encodes a transmembrane protein consisting of a putative PEBP-like domain, a putative TNFR/NGFR family cysteine-rich domain and a VWFC module. A C to A mutation in its second exon changed a cysteine codon (TGC) in Chuan 7 to a termination codon (TGA) in Minghui 63 which yields a premature termination and a 178-aa truncation in the C-terminus. Overexpression of *GS3* not only produces short grains but also results in reduced plant size, including shortened height, leaves, and panicles, suggesting its role as a negative regulator with pleiotropic effects (Mao et al., 2010).

GW2 was the second cloned major QTL for grain size in rice (Song et al., 2007). This QTL was identified and molecularly characterized from a F2 population derived from a *japonica* × *indica* cross (WY3 × Fengaizhan-1). GW2 encodes a RING protein with E3 ubiquitin ligase activity. Compared with the Fengaizhan-1 allele at locus GW2, the WY3 allele has a 1-bp deletion in exon 4, resulting in a premature stop codon which leads to truncation of 310 amino acid residues. This loss-of-function mutation produces substantially more and longer cells in outer parenchyma cell layer of the spikelet as well as larger endosperm cells and accelerated grain filling. Additionally, the WY3 allele increases grain size and yield with little influence on eating or cooking quality making it a useful QTL in breeding.

GS5, the first cloned positive regulator, controls grain size by regulating grain width, filling and weight in rice (Li et al., 2011). Primary QTL mapping detected this QTL on the short arm of chromosome 5 in a doubled haploid (DH) population derived from the

cross between Zhenshan 97 (large grain size) and H94 (small grain size). Fine mapping resolved *GS5* to a candidate region of 11.6-kb in length where there was only one predicted open reading frame (ORF). This ORF has ten exons and encodes a putative serine carboxypeptidase. *GS5* positively regulates grain size by increasing cell number in the inner parenchyma cell layer and the cell size of palea and *GS5* is further shown to be a positive modulator upstream of cell cycle genes whose expression is significantly elevated when *GS5* is overexpressed. The observed grain size and yield difference between Zhengshan 97 (large grain size) and H94 (small grain size) was due to the polymorphisms in the GS5 promoter region where strong/weak promoters were associated with high/low yield. The Zhengshan 97 allele was expressed with more abundance in the palea/lemma at 2, 4 and 5 day before heading and in the endosperm at 10 days after fertilization which corresponded well with critical stages for grain width and grain filling.

GRAIN INCOMPLETE FILLING 1 (GIF1) was the first cloned and functionally analyzed QTL for grain-filling (Wang et al., 2008). *GIF1* is located on chromosome 4 and encodes a cell-wall invertase required for carbon partitioning during early grain-filling. Specifically, GIF1 unloads sucrose in the ovular and stylar vascular tissues for starch synthesis in the endosperm during grain-filling. The *gif1* mutant has a 1-nt deletion in the coding region which results in a premature stop and reduced grain weight. During grain filling, the wild-type *GIF1* allele is expressed in the ovular vascular trace, pericarp and endosperm tissues. In contrast, the cultivated *GIF1* allele is mainly confined to the ovular trace which leads to a higher accumulation level of glucose, fructose and sucrose and,

hence, increased grain weight. This restricted expression pattern of cultivated *GIF1* gene is caused by accumulated mutations in its promoter region during rice domestication both in *japonica* and *indica*.

Plant architecture

The generalization of dwarfing genes in wheat and rice cultivars was crucial to the success of the Green Revolution. *Reduced height-B1b (Rht-B1b)* and *Reduced height-D1b (Rht-D1b)* are known as the green revolution genes in wheat (Peng et al., 1999). Their wild-type alleles *Rht-B1a* and *Rht-D1a* encode DELLA proteins which are transcriptional regulators that repress gibberellin (GA)-responsive growth. *Rht-B1b* and *Rht-D1b* both contain single nucleotide substitutions causing premature stop codons in the N-terminal coding region leading to truncated proteins with increased repression of GA signal transduction. *semidwarf-1 (sd-1)* is known as the green revolution gene in rice and encodes gibberellin 20-oxidase (GA20_{ox}) which is an enzyme catalyzing three intermediate steps of reactions converting GA precursors to GA (GA₅₃ \rightarrow GA₄₄ \rightarrow GA₁₉ \rightarrow GA₂₀) (Monna et al., 2002; Sasaki et al., 2002). Its widely-used allele is from the Chinese cultivar, Dee-geo-woo-gen that contains a 383-bp deletion in the GA20ox gene (known as *OsGA200x2*) resulting in a premature stop codon and a highly truncated inactive enzyme (Hedden, 2003).

MONOCULM 1 (MOC1) is the first cloned key regulator of rice tiller number (Li et al., 2003). A screen of mutants with altered tiller numbers identified a rice plant with only one main culm, named *monoculm 1 (moc1). moc1* is caused by a recessive mutation at a single locus and was mapped to the chromosome 6 of rice. *MOC1* encodes a plant-

specific GRAS family nuclear protein and is mainly expressed in the axillary buds to initiate axillary buds and to promote their outgrowth. Rice plants with enhanced expression of *MOC1* produced more tillers as expected. In contrast, *moc1* is not able to initiate axillary meristem and therefore, has only one main culm.

Rice *Narrow leaf 1(Nal1)* encodes a plant specific protein preferentially expressed in vascular tissues with rich abundance (Qi et al., 2008). A 30-bp deletion in its coding region is significantly associated with reduced polar auxin transport capacity and affects the distribution pattern of vascular bundles leading to narrower leaves with fewer longitudinal veins. *NARROW AND ROLLED LEAF 1 (NRL1)* was mapped to chromosome 12 in rice. It encodes the cellulose synthase-like protein D4 (OsCsID4) which plays a crucial role in leaf expansion in rice (Hu et al., 2010). Its three mutants (single base substitutions at three different loci) *nrl1-1, nrl1-2, and nrl1-2* are smaller and show erect, narrow and semi-rolled leaves compared to the *NRL1* genotype.

Spike morphology

Grain number per panicle is one of the most important yield components in cereals. The first cloned QTL for grain number per panicle was Gn1a in rice (Ashikari et al., 2005). This QTL was mapped by using 96 backcross inbred lines derived from the cross between Habtaki (higher grain number) and Koshihikari (lower grain number). A major QTL contributed by Habataki explained 44% of the grain number variation and was identified on chromosome 1. This QTL was further fine-mapped to a region of 6.3 kb, where there was only one predicted open reading frame. Molecular characterization of Gn1a showed that it encodes a cytokinin oxidase/dehydrogenase (OsCKX2) whose

reduced expression causes cytokinin accumulation in the inflorescence meristem and increases the number of reproductive organs which leads to higher grain number per panicle enhancing grain yield. Based on comparative genomics, TaCKX6-D1 a wheat ortholog of the rice OsCKX, was cloned and located on the wheat chromosome 3D (Zhang et al., 2012). This gene was mapped by using a set of 199 RILs derived from a cross between two Chinese Spring cultivars Yanzhan1 and Neixiang188. The Yanzhan1 allele, named TaCKX6-D1a, has an 18-bp indel in its second intron where the Neixiang188 allele, named TaCKX6-D1b, has an insertion in this region. TaCKX6-D1a is associated with higher 1000-grain weight and its additive effect is $1.3\sim1.4$ g per 1000 grains. Four more alleles of TaCKX6-D1 were found and named TaCKX6-D1e. Evolutionary analysis showed that alleles c, e and d are ancient haplotypes occurring only in the wild species, whereas alleles a and b are newly derived, present most commonly in both modern cultivars and landraces.

Quantitative trait loci *WFP (WEALTHY FARMER'S PANICLE)* and *IPA1 (IDEAL PLANT ARCHITECTURE)* were cloned in the same year by two research groups independently and were found to share the same underlying gene *OsSPL14* (Jiao et al., 2010; Miura et al., 2010). *OsSPL14* is located on the chromosome 8 of rice and encodes a plant-specific transcription factor SQUAMOSA PROMOTER BINDING PROTEIN-LIKE (OsSPL14) which is conserved in sorghum, wheat, maize and *Arabidopsis thalinana* (Miura et al., 2010). Higher expression of *OsSPL14* promotes panicle branching in the reproductive stage. Sequence analysis showed that *OsSPL14* contains a microRNA-targeted sequence in the third exon (targeted by OsmiR156). OsmiR156 is

highly expressed in the vegetative stage and cleaves the *OsSPL14* mRNA suppressing the expression of *OsSPL14*. In the reproductive stage, OsmiR156 disappears leading to a higher expression level of *OsSPL14* and the subsequent enhanced primary branching on the panicle.

DEP1 is the first cloned QTL that acts through the determination of panicle architecture (Huang et al., 2009). *DEP1* is located on chromosome 9 of rice and encodes a phosphatidylethanolamine-binding protein-like domain protein. Its dominant loss-of-function allele *dep1* from cultivars such as Nanjing 11 and Nipponbare produces erect panicles with a shorter inflorescence internode, increased number of both primary and secondary panicle branches and increased number of grains. Although the 1000-grain weight of NIL-*dep1* was slightly lower than that of NIL-*DEP1* plants, the overall grain yield of NIL-*dep1* in wheat, showed a longer panicle with fewer spikelets suggesting that this locus and its homologs in other small grain cereals may provide an option for increasing grain yield.

Ghd7 is the first cloned quantitative trait locus that controls grain numbers per panicle, plant height and heading date simultaneously (Xue et al., 2008b). *Ghd7* was mapped on chromosome 7 of rice using both $F_{2:3}$ and RIL populations derived from a cross between Zhenshan 97 (lower grain number and days to heading) and Minghui 63 (higher grain number and days to heading). *Ghd7* encodes a CCT (CO, CO-LIKE and TOC1) domain protein. However, comparison with other CCT domain-containing proteins showed that t

GHD7 is distinct from all other members of the CCT domain protein family and is considered to be an evolutionary new gene in the lineage. *Ghd7* is a key upstream transcription factor in the photoperiod flowering pathway and its Minghui 63 allele allow rice plants to fully utilize light and temperature by delaying flowering under long-day conditions. As a result, larger panicles with more grain numbers occur. Furthermore, the Minghui 63 allele is mainly expressed in young tissues and also has a positive effect on stem growth by producing more nodes, a longer upper-most internode and thicker stems with improved lodging resistance. All these pleiotropic effects contribute to a high grain yield. *Ghd8* is a major QTL on chromosome 8 with similar pleiotropic effects as *Ghd7* (Yan et al., 2011). *Ghd8* encodes the OsHAP3 subunit of the HAP complex and acts upstream of rice florigen genes *Fhd1*, *Hd3a*, and *RFT1*. In addition, *Ghd8* has a positive effect on rice tiller number, primary and secondary branches, by up-regulating *MOC1* which is a key gene controlling tillering and branching.

OTL mapping and cloning in breeding programs

Basics of QTL Mapping

Historically, genetics relied entirely on phenotypic information to determine the relative importance of genetic versus environmental factors through techniques such as analysis of variance and heredity analysis (Walsh, 2001). However, merely based on phenotypic evaluation, it is generally not possible to identify relevant loci influencing a trait. The development and combination of genetic marker technologies, molecular biology and biometric methods has made QTL mapping possible in complex traits studies.

OTL mapping is a set of statistical methods attempting to explore the relationship between DNA sequence variation and natural phenotypic variation for quantitative or complex traits and is widely utilized in modern genetics (Haley, 2002; Kearsey and Farquhar, 1998; Majumder and Ghosh, 2005; Myles et al., 2009). By combining phenotypic data (trait measurements) and genotypic data (usually molecular markers), QTL mapping allows researchers to link certain complex phenotypes to specific regions of chromosomes (Miles and Wayne, 2008). Although the principles of QTL mapping have been known since the early twentieth century, genetic dissection of complex traits was limited to a few model organisms due to the lack of polymorphic markers (Mackay et al., 2009). Since the discovery of abundant molecular markers in late 1980s, advances in rapid and cost-effective genotyping methods and the employment of statistical methods have revolutionized the field of QTL mapping (Mackay et al., 2009). Statistical methods developed for QTL mapping are based on homologous recombination at meiosis, during which the genetic material is exchanged by crossing over (Myles et al., 2009; Nordborg and Weigel, 2008).

To perform QTL mapping for a measurable quantitative trait, a mapping population and linkage map are needed. Coupling this map with phenotypic data for the trait (e.g. yield) allows the region of the genome associated with the phenotype to be identified. Therefore, the three requirements for QTL mapping are: 1) a mapping population where individuals differ genetically with regard to traits of interest; 2) genetic markers that distinguish these lines; and 3) quantitative data for the traits to be explored; (Miles and Wayne 2008).

Mapping population

In plant breeding, the most common mapping populations include F_2 , recombinant inbred lines (RILs), and doubled haploids (DH). The simplest form of a mapping population is a collection of F_2 plants derived directly by selfing a F_1 plant. In this case, the expected segregation ratio for each codominant marker is 1:2:1 (homozygous like P1:heterozygous:homozygous like P2) (Schneider, 2005). However, an F_2 populations can only be used once since they are not immortal and generally cannot be clonally propagated (Schneider, 2005). This makes phenotypic evaluation in multi-location/year difficult to perform.

Recombinant inbred lines (RILs) are generated by repeated selfing of F_2 individuals for at least six generations using the single seed descent method (Snape and Riggs, 1975). Once established, RILs can be propagated eternally and shared by other groups in the research community (Broman, 2005). A second advantage of RILs is that after several rounds of meiosis before homozygosity is reached, the degree of recombination and the resolution of the linkage map are both higher compared to that of F2 populations and the map positions of even tightly linked markers can be determined (Schneider, 2005). Despite the fact that RILs are among the most effective population designs, it is time consuming to construct homozygous RIL populations, typically requiring at least six generations of self-fertilization starting from a heterozygous F_1 (Seymour et al., 2012).

Another option for mapping is to develop a doubled haploid (DH) population. Haploid gametes produced from F_1 meiosis contain all recombination information but only half

the number of chromosomes. To make a DH population in plants, F₁ flowers are pollinated with incompatible pollen, leaving a haploid embryo. After embryo rescue and tissue culture, haploid seedlings are treated with colchicine, preventing cytokinesis after mitosis and leading to doubled haploids (Schneider, 2005). Each DH contains two identical sets of chromosomes in each cell and is completely homozygous at every locus. This time-efficient process can be finished in only two steps and has been widely used in QTL mapping in a variety of species, especially in grasses (Seymour et al., 2012).

Genetic markers

Genetic markers are heritable biological features that are determined by allelic forms of genes or genetic loci and can be measured in one or more populations (Davey et al., 2011; Xu, 2010). Thus, they can be used as experimental probes or tags to keep track of an individual, a tissue, a cell, a nucleus, a chromosome or a gene and are the cornerstone of modern genetics (Davey et al., 2011; Xu, 2010). As Xu (2010) summarized, genetic markers fall into two categories: 1) classical markers and 2) DNA markers. Classical markers include morphological markers, cytological markers and biochemical markers. DNA markers include randomly amplified polymorphic DNA (RAPD), simple sequence repeats (SSR) or microsatellites, amplified fragment length polymorphisms (AFLP), single nucleotide polymorphisms (SNP), and diversity arrays technology markers (DarT).

After the first identification and use of DNA-based molecular markers in 1980s, such as restriction fragment length polymorphism (RFLP), the development and use of molecular markers has increased explosively in human genetics, plant breeding and genetics, animal breeding and genetics, and germplasm characterization and management (Botstein et al.,

1980; Jiang, 2013). This technological revolution began with low-throughput RFLP and culminated with SNPs in recent years (Gupta et al., 2008). First identified in the human genome, SNPs make up about 90% of all human genetic variation, happen every 100–300 bases, and have been proven to be universal in plant and animal systems as well (Wang, 1998; Xu, 2010). SNP identification is usually achieved by aligning genomic or expressed sequence tag (EST) sequences available in databases, or via next-generation sequencing (NGS)-based sequencing or resequencing of candidate genes/ PCR products and even whole genomes in more than one genotype (Gupta et al., 2008). Once discovered, many platforms are available to carry out SNP genotyping, such as Genechip, Infinium II and Goldengate (Kumar et al., 2012).

In crop plants, abundant and high-density SNPs can accelerate high-density genetic mapping and identification of genes/QTLs for traits of economic and agronomic importance as well as the application of marker-assisted breeding and genomic selection (Trebbi et al., 2011). Recently, SNP discovery has been reported in many crop plants such as rice, maize, barley, wheat, and sunflower (Bachlava et al., 2012; Cavanagh et al., 2013; Close et al., 2009; Ganal et al., 2011; Hu et al., 2013; McCouch et al., 2010). For example, Trebbi et al. (2011) discovered and validated a set of 275 SNPs in durum wheat using 12 durum cultivars through complexity reduction of polymorphic sequences (CroPS) technology and Illumina Golden Gate technology. Ganal et al. (2011) developed a large maize SNP array containing 57,838 markers across the genome, out of which 49,585 markers, representing 17,520 genes were storable and of good quality for further

genotyping. Additionally, using the RICE6K SNP array, Hu et al. (2013) mapped 5 novel QTLs for rice grain shape for marker-assisted selection in rice.

Genotyping by sequencing

The decreasing cost of next-generation sequencing (NGS) makes high-throughput genome-wide genetic marker discovery applicable not only to model organisms with reference genome sequences but also to non-model species without genome data (Davey et al., 2011). Recently, genotyping by sequencing (GBS), a low coverage genotyping method suitable for high diversity and large genome species, was proposed. It is reported to be "simple, quick, extremely specific, highly reproducible, and may reach important regions of the genome that are inaccessible to sequence capture approaches" (Elshire et al., 2011). Compared with restriction-site-associated DNA sequencing (RAD-seq), GBS has simpler library preparation protocols but produces equivalent results at a very low cost per sample (Davey et al., 2011). After the digestion of genomic DNA with restriction enzymes, barcode and common adapters are ligated to sticky ends of digested DNA fragments after which samples can directly go to PCR amplification followed by DNA sequencing (Elshire et al., 2011). Since no fragment size selection and few enzymatic and purification steps are involved, this protocol is time and cost efficient (Elshire et al., 2011). In maize, for example, 200,000 markers were identified and mapped in a very short time at a cost of \$8,000 (Elshire et al., 2011). During this study, GBS was coupled with multiplex technology and simultaneously processed up to 2,688 samples per sequencing run (384 samples per channel \times 7 channels) (Elshire et al., 2011).

Statistical models for linkage mapping

Traditionally, QTL detection is achieved by linkage mapping, where two homozygous inbred parental lines are crossed to create a mapping population/family and attempts are made to identify cosegregation of genetic markers and phenotypes within this family (Myles et al., 2009).

In the late 1980s, markers and advances in genotyping technology led to the development of statistical methods for use in QTL mapping of complex quantitative traits. A landmark method for QTL mapping is interval mapping (IM) (Lander and Botstein, 1989). This method established a statistical framework for most methods that are currently used to analyze QTLs of complex traits (Xu and Zhu, 2012). In IM, phenotypic data is used to compute a log likelihood (LOD) value at a DNA marker interval. As the marker interval slides along the chromosome (genome scanning), LOD values change accordingly. A OTL associated with a quantitative trait is assumed to be located on the genome under the peak where the LOD is higher than a specified threshold. The precision of IM was improved by including associated markers as covariant variables (Zeng, 1994). This method is known as composite interval mapping (CIM). Under the assumption of no QTL× environment interaction, CIM can produce unbiased estimations of QTL positions and effects. The IM and CIM methods have been widely applied in experimental populations, such as F₂, recombinant inbred lines (RIL), and doubled haploids (DH) (Xu and Zhu, 2012). Other well-recognized mapping models include multiple interval mapping (MIM) (Kao et al., 1999), inclusive composite interval mapping (ICIM) (Li et al., 2007a), conditional QTL mapping (Wen and Zhu, 2005; Zhu, 1995), and QTL mapping based on mixed linear model (Wang et al., 1999; Yang et al., 2007).

Linkage mapping, however, has its own drawbacks. It is based on a highly controlled population structure that goes through relatively few meiosis events. Therefore, recombination has not had sufficient time to shuffle and rearrange the genome and QTLs may end up in large chromosomal regions making it difficult to capture the precise location of promising QTLs and to distinguish pleiotropic effects of a single QTL from multiple independent linked QTLs (Xu, 2010). The resulting low precision can be partially improved by using a larger mapping population with more recombination events and a high-density marker coverage across the genome. Lastly, due to this rigid population structure, QTLs identified in linkage mapping populations are usually limited to specific crosses and may not be generalized to other populations.

Association mapping

In association mapping, genotype data and phenotype data are collected from a natural population (assuming random mating) where the experimenter has no control over the structure of the mapping population (Myles et al., 2009). This advantage leads to its enormous success in human disease research, for which obtaining a controlled population is almost impossible (Collins, 2007). Association mapping employs historical recombination events that have happened between QTLs and marker alleles providing higher mapping resolution and thus requires a smaller number of individuals compared with linkage mapping (Mackay et al., 2009). The application of association mapping expanded enormously with the advent of next generation sequencing technology which

has the capacity of discovering, sequencing and genotyping large numbers of molecular markers, mostly SNP, across almost any genome of interest in a short time and in a costeffective manner (Davey et al., 2011). Having the whole genome covered with molecular markers enables researchers to conduct genome-wide association studies with revolutionary resolution.

A randomly mating population, however, almost does not exist in practice and this nonrandom mating population structure can generate complex patterns of population structure and relatedness in plants which is a strong confounding factor, especially for the traits that are to be introgressed into local cultivars (Myles et al., 2009; Nordborg and Weigel, 2008). Despite the fact that statistical methods have been developed to correct for various types of relatedness, one should recognize that these methods are still subject to further improvement (Myles et al., 2009). In addition, association mapping cannot detect alleles with low frequency in the population, even if they have a large effect on the phenotype (Davey et al., 2011). However, population genetics suggests that, in the majority of species, most alleles are rare, which makes it difficult to explain phenotypic variation via association mapping. (Myles et al., 2009). Thus, biparental mapping is still an important tool.

The power of association mapping highly depends on the strength of the association between molecular markers and the corresponding functional variants/QTLs, which is known as linkage disequilibrium (LD). LD happens, considering two separate loci located on the same chromosome, when the presence of the genotype at one locus is not independent of the other. In other words, they are linked and tend to occur together. Since it is described through DNA recombination, the strength of LD is a function of the distance between two loci: the closer they are, the stronger the LD (Mackay and Powell, 2007). In association analysis, the final mapping resolution relies on the decay of LD over distance, which differs both between and within species (Collins, 2007). Therefore, association mapping may have less power when performed on a bi-parental mapping population where LD is higher.

Cloning QTLs in wheat

To breeders, QTL cloning is not a routine option and is economical only for those loci with clear added value (Salvi and Tuberosa, 2007). Only a very few QTLs in bread wheat have been cloned through map-based cloning and the underlying gene characterized (Liu et al., 2013; Uauy et al., 2006). QTL cloning in wheat is challenging partly because of its large and complex genome and the lack of a high quality reference sequence. This issue could be addressed by synteny.

Cereal genomes show substantial conservation in gene order, known as synteny or colinearity (Akhunov et al., 2013; Dubcovsky et al., 2001; Qi et al., 2013; Sorrells et al., 2003). This has great important applications. For example, Akhunov et al. (2013) used the syntenic relationships between wheat and *Brachypodium distachyon*, rice, and sorghum to order contigs and scaffolds of wheat chromosome 3A. Salse et al. (2008) studied the evolution of grasses through comprehensive analysis of intragenomic duplications and comprehensive synteny. However, macro-collinearity does not always predict micro-colinearity (Sorrells et al., 2003). An abundance of rearrangements,

insertions, deletions, and duplications exist when grass genomes are compared (La Rota and Sorrells, 2004). Therefore, for QTL cloning, synteny is mostly reliable when a relatively small genomic region is examined.

In general, four steps are generally involved in cloning a QTL in wheat. First, a biparental population is used to locate a QTL and its flanking markers on a certain chromosome. Second, a fine-mapping population derived from a cross between two parents differing only in the flanking marker-defined region is used to construct a precise genetic map indicating the position of the QTL of interest. In this step, the QTL is physically mapped to one of wheat's deletion bins based on the physical position of its flanking markers (Abeysekara et al., 2010; Hua et al., 2009). Wheat geneticists have developed a collection of deletion stocks that physically dissect wheat chromosomes into bins (Endo and Gill, 1996). A number of simple sequence repeats (SSRs) and expressed sequence tag (ETSs) are also physically mapped to these deletion bins through Southern hybridization experiments (Qi et al., 2004; Sourdille et al., 2004). Thirdly, the sequences of the ESTs that mapped to the same deletion bin with the QTL of interest are used as query sequences to search the rice and *Brachypodium distachyon* genome sequences to identify a collinear region. Namely, saturation mapping via synteny (Zhang et al., 2013). Rice and Brachypodium distachyon genes residing within a colinear region are used to search the wheat ESTs database to identify previously unmapped ESTs to saturate the flanking marker-defined region. The fourth step involves sequencing BAC clones (Liu et al., 2013). After saturation mapping, the QTL region is narrowed down. The two closest flanking markers are used to screen BAC libraries and chromosome walking as well as

sequencing of the target interval leads to the identification of candidate genes (Krattinger et al., 2009).

Trends in wheat breeding

High-throughput phenotyping

Linking genotypic variation to observed traits/phenotypes is essential for marker assisted selection and breeding by design in breeding practice (Peleman and van der Voort, 2003; Tester and Langridge, 2010). The rapid development of genomics-based genotyping technologies in the past decade, especially sequencing capability, has offered breeders powerful tools and resources to access a wealth of genomic information on a breeding population at a relatively low cost (Davey et al., 2011). In contrast, phenotyping a large breeding population for multiple traits at multiple environments is still technically challenging and laborious (Furbank and Tester, 2011). The lack of access to high-throughput and high-dimensional phenotypic data on organism-wide scale has become a new bottleneck that limits our ability to dissect the genetics of quantitative traits in both crop improvement and basic research (Houle et al., 2010).

Interest in developing high-throughput phenotyping platforms (HTPPs) has arisen from both private and public sectors to address the issue (Araus and Cairns, 2014). Collaborative networks have formed to build HTPPs. Some of the most advanced and fully automated public facilities for indoor experimentation include the Australian Plant Phenomics Facility and the European Plant Phenotyping Network. These platforms are equipped with robotics, conveyor systems, imaging stations, watering stations, and computing infrastructure and are able to operate automatically to collect data for 3D plant

canopy architecture, canopy temperature, leaf color and morphology, and photosynthesis at different developmental stages (http://www.plantphenomics.org.au; http://www.plantphenotyping-network.eu). Under field conditions, HTPPs employs, mostly, remote sensing and imaging and near-infrared reflectance spectroscopy analysis to finish rapid assessment of traits such as vegetation indices at more or less frequent intervals during the crop cycle (Araus and Cairns, 2014). Field HTPPs carry multiple sets of sensors and often use high-clearance tractors, cable robots, helicopters, aerostats, and drones as sensor carriers (White et al., 2012). Accurate and rapid phenotypic data produced on HTTPs (indoor and outdoor) helps breeders and crop scientists to exploit genomic information and gain new insights that are hard or unable to access before. For example, rice researchers built a high-throughput rice phenotyping facility and demonstrated that, when combined with genome wide association studies, high-throughput phenotyping better dissected the genetic architecture of rice complex traits such as shoot weight and green leaf area than traditional manual measurements (Yang et al., 2014). In addition, an image-based high-throughput field phenotyping system for crop roots was developed and identified 13 new plant root traits that differentiated nine maize genotypes 8 weeks after planting (Bucksch et al., 2014). High-throughput genotyping is emerging as a new crop breeding frontier and is revolutionizing many areas of plant science (Araus and Cairns, 2014; Kloth et al., 2015; Klukas et al., 2014).

Genomic selection

Prediction of crop performance as a function of genetic architecture is a major challenge for crop research (White et al., 2012). Marker-assisted selection (MAS) has been successfully and efficiently used to select elite cultivars with desired qualitative characters such as enhanced disease resistance. However, since MAS has traditionally relied on markers linked to large-effect quantitative trait loci (QTL), it has been less effective for quantitative traits that are complex and controlled by many genes with small effects (Jannink et al., 2010). Genomic selection has been proposed and implemented as a new breeding approach to address the deficiency of MAS and to accelerate genetic gains in plant and animal breeding (Crossa et al., 2014; Meuwissen et al., 2001). In contrast to MAS, genomic selection simultaneously estimates the allelic effects of all available markers spread across the genome to predict phenotypic performance and does not test the significance of a link between a marker and a QTL (Massman et al., 2013).

Genomic selection first uses a 'training population' of individuals that have been both genotyped and phenotyped to produce genomic estimated breeding values (GEBVs) for each marker which are further used by a prediction model to predict the performance of a 'candidate population' from which individuals are only genotyped and, then, selected based on their GEBVs for advancement in the breeding cycle (Jannink et al., 2010). Genomic selection has been evaluated with simulation data and real data in dairy cattle (Hayes et al., 2009), mice (Legarra et al., 2008), rye (Wang et al., 2014), sugar beet (Wurschum et al., 2013), rice (Xu et al., 2014), wheat (Poland et al., 2012), and maize (Crossa et al., 2013). The correlation between true breeding value and the estimated breeding value has reached levels of 0.85 even for polygenic low heritability traits (Heffner et al., 2009). With its continuously improved prediction accuracy, genomic selection could dramatically change the role of phenotyping from selecting lines to updating prediction models and substantially accelerate the breeding cycle (Heffner et al.,

2009; Morrell et al., 2012). It is expected that genomic selection will revolutionize plant and animal breeding in the next decade (Henryon et al., 2014; Morrell et al., 2012).

Synthetic wheat

Hexaploid wheat evolved from the hybridization between T. turgidum (AABB) and Ae. tauschii (DD). It is believed that only a limited number of these two donor species were involved in the speciation process and, thus, the genetic diversity of hexaploid wheat was largely reduced (Yang et al., 2009). To address this evolutionary bottleneck and introduce favorable alleles into hexaploid wheat from its wild relatives, synthetic wheats have been made via artificial synthesis of hexaploid wheat (*T.turgidum* \times *Ae. tauschii*) in a manner analogous to the natural evolution of hexaploid wheat (Trethowan and van Ginkel, 2009). Many of these wild species, especially Ae. tauschii, possess novel and elite genes for biotic and abiotic stresses which can provide synthetic wheat with exceptional disease resistance and stress tolerance (Dreisigacker et al., 2008; Jia et al., 2013b). In addition, synthetic wheat is also a valuable source of alleles to improve grain yield and yield components (del Blanco et al., 2001). Since the early 1990s, the International Maize and Wheat Improvement Center (CIMMYT) has started making synthetic wheat and transferring favorable traits to CIMMYT elite breeding lines (Dreisigacker et al., 2008). To date, more than 1000 synthetic wheats have been produced by CIMMYT and are being used by breeding programs worldwide (Dreisigacker et al., 2008; Yang et al., 2009). Synthetic wheat and synthetic wheat-derived cultivars have great potential for enhancing grain yield and adaptation of modern hexaploid wheat (Li et al., 2014; Trethowan and van Ginkel, 2009). Thus, a new generation of wheat varieties produced from synthetic wheats is on the horizon (van Ginkel and Ogbonnaya, 2007).

Chapter 2: Quantitative trait loci mapping of grain yield in a doubled haploid population of soft red winter wheat <u>Abstract</u>

Understanding the genetic basis of grain yield and yield components is the key to improving grain yield potential in common wheat (Triticum aestivum L.). My objective was to identify quantitative trait loci (QTL) associated with grain yield (GYLD), spikes m⁻² (SPSM), grain weight per spike (GWPS), grains per spike (GPS) and thousand-grainweight (TGW) using a doubled haploid (DH) population. The DH population was evaluated in five environments and was genotyped with single nucleotide polymorphism (SNPs), simple sequence repeats (SSRs), and a morphological marker. The linkage map spanned 1977.6 cM with an average interval length of 2.3 cM. Sixty four putative QTLs for GYLD, SPSM, GWPS, and GPS were detected on eighteen wheat chromosomes. The phenotypic variance explained by these QTLs ranged from 3.7% for GWPS to 71.2% for TGW. The major GYLD QTL (QYld.cz-3B.2) and TGW QTL (QTgw.cz-7A.5) identified in the present study explained 21.2% and 71.2% of the phenotypic variation, respectively. GYLD QTLs closely linked to *Fhb1* and *Ppd-D1* genes were identified. Eleven QTLs exhibited pleiotropic effects. A genomic region with significant pleiotropic effects for GYLD, SPSM, GWPS, and GPS was located on 1A. In addition, $QTL \times$ environment interaction, epistasis and epistasis × environment interactions were detected. Major QTLs identified in this study could be used in marker-assisted breeding to increase grain yield or QTL fine mapping.

Introduction

Wheat (*Triticum aestivum* L.) is the staple food for more than 40% of the world's population. Increasing wheat production is essential to meet the demand of wheat consumption from an increasing population worldwide. As one of the key economic drivers behind the wheat cropping enterprise, improving grain yield potential is a major goal in both public and private breeding programs (Kuchel et al., 2007b). Grain yield is a resultant complex trait influenced by many processes that involve vegetative and reproductive growth and developmental stages (Yoshida, 1972). Grain yield is determined by yield component traits, such as grains per spike (GPS), spikes m⁻² (SPSM), grain weigh per spike (GWPS), thousand-grain-weight (TGW) and affected by other yield related traits, e.g. plant architecture. Yield and yield component traits are genetically controlled by multiple quantitative trait loci (QTL) with major and minor effects that are highly influenced by environmental conditions (Deng et al., 2011; Kumar et al., 2007).

Identification of QTLs on specific chromosomes for yield and yield components can facilitate incorporating these traits into regionally adapted cultivars in an effective manner through marker assisted selection (MAS) (Carter et al., 2011). This allows breeders to test for the presence and to track down the proven QTL by targeting its closely linked markers for a more efficient and accurate selection of superior cultivars (Kuchel et al., 2007b). A large number of QTL studies have been reported in wheat (Heidari et al., 2011; Kuchel et al., 2007b; Kumar et al., 2007; Wu et al., 2012) and QTLs for grain yield and yield components have been identified in all wheat chromosomes

mostly with minor genetic effects (Wu et al., 2012; Zhang et al., 2010). For example, using two wheat mapping populations, Kumar et al. (2007) detected eighty-six QTLs out of which six were pleiotropic/coincident involving more than one yield related trait. Kuchel et al. (2007b) found in a DH population that although the higher yielding parent contributed most of the favorable alleles, the lower yielding parent also possessed higher yielding QTLs based on the data from eighteen environments. Li et al. (2007b) identified five environment-specific QTLs for GYLD on chromosome 1D, 2D, and 3B explaining 10.4-23.0% of the phenotypic variation. Groos et al. (2003) reported a stable QTL for TGW on chromosome 2B which explained up to 20% of the phenotypic variation in seven trials. Interestingly, the favorable allele was from Récital, the parental line with lower TGW. Heidari et al. (2011) identified a genomic region on chromosome 1A for GPS explaining up to 22.4% of the phenotypic variation in two environments and three QTLs for SPSM on chromosome 1A, 7A, and 2D explaining up to 21.4% of the phenotypic variation. Several large-effect loci affecting grain yield per se such as *Rht1* and *Ppd-D1* have been cloned and molecularly characterized (Boden et al., 2015; Pearce et al., 2011). One locus, TaCKX6-D1, significantly associated with TGW in wheat was isolated and shown to be orthologus to rice gene OsCK2. Moreover, yield component traits are less environmentally sensitive and generally exhibit higher heritability than grain yield, as a result of which, indirect selection on yield component traits tends to result in higher stable genetic gain than direct selection for grain yield (Kumar et al., 2007; Wu et al., 2012). Therefore, examining yield components when evaluating grain yield per se is necessary for sustained yield potential improvement (Wu et al., 2012).

Additionally, additive main effects, digenic epistasis, $QTL \times$ environment interactions (additive \times environment interaction and epistasis \times environment interactions) also are crucial factors determining the expression of quantitative traits (Mackay, 2001). In classical Mendelian genetics, the masking of genotypic effects at one locus by genotypes of another is called epistasis which is also broadly used to indicate any statistical interaction between genotypes at two (or more) loci in quantitative genetics (Mackay et al., 2009). Epistasis can be synergistic or antagonistic depending on whether the effect of one locus is enhanced or suppressed by the second locus (Mackay, 2001). As a result, the phenotype of a certain genotype would not be a simple sum of the additive effects of all loci involved. When plants are challenged by fluctuations in environmental conditions, both additive and epistatic effects of the same loci are modified to some extent so that plants can adapt to new situations by changing its phenotypic expression, known as phenotypic plasticity (El-Soda et al., 2014). A thorough understanding of the interactions mentioned above in breeding populations would help breeders predict the performance of genotypes across years and locations with more confidence. However, due to the lack of appropriate methodology and easy-to-use statistical software, QTL detection was typically conducted under the assumption of additive main effects only until the mixedmodel based composite interval mapping (MCIM) was developed (Wang et al., 1999). MCIM showed high accuracy and power in mapping QTLs with epistatic effects and $QTL \times$ environment interactions by using the best-linear-unbiased prediction (BLUP) method (Wang et al., 1999) and has been well accepted ever since (Li et al., 2007b; Xing et al., 2002; Zhang et al., 2009). Another big constraint in accurate QTL mapping and subsequent application of MAS was the lack of fast and large-scale genotyping platform

as the cost of initial genotyping approaches were high. A recent development in DNA marker technology is single nucleotide polymorphisms (SNPs). In contrast to traditional simple sequence repeats (SSRs) and amplified fragment length polymorphisms (AFLPs), SNPs are more abundant across genomes of many species and constitute $\sim 90\%$ of the genetic variation in virtually all organisms (Gupta et al., 2008). Recently, SNP discovery and QTL mapping using SNPs have been reported in many crop plants such as rice, maize, barley, wheat, and sunflower (Bachlava et al., 2012; Cavanagh et al., 2013; Close et al., 2009; Ganal et al., 2011; Hu et al., 2013; McCouch et al., 2010). Trebbi et al. (2011) discovered and validated a set of 275 SNPs in durum wheat using 12 durum cultivars through complexity reduction of polymorphic sequences (CroPS) technology and Illumina Golden Gate technology. Ganal et al. (2011) developed a large maize SNP array containing 57,838 markers across the genome, out of which 49,585 markers, representing 17,520 genes were storable and of good quality for further genotyping. This SNP array was then used to genotype two recombinant inbred line populations and two high density linkage maps were also established with 20,913 and 14,524 markers respectively. Moreover, using the RICE6K SNP array, Hu et al. (2013) mapped five novel QTLs for rice grain shape. Furthermore, genotyping by sequencing (GBS) is a new SNP genotyping method suitable for high diversity and large genomes and has shown to be "simple, quick, extremely specific, highly reproducible, and may reach important regions of the genome that are inaccessible to sequence capture approaches" (Elshire et al., 2011). Compared with other sequencing-based genotyping method such as restrictionsite-associated DNA sequencing (RAD-seq), GBS has simpler library preparation protocols but produces equivalent results at very low cost per sample (Davey et al.,

2011). Coupling GBS with multiplex technology, up to 2,688 samples/breeding lines can be processed simultaneously per sequencing run (Elshire et al., 2011). In maize, for example, 200,000 markers were identified and mapped in a very short time at a cost of \$8,000 (Elshire et al., 2011).

High grain yield of any crop can be achieved only when a proper combination of cultivar, environment, and agronomic practices is obtained (Yoshida, 1972). Understanding the genetic effects of QTLs, how QTLs interact with each other, and how these QTLs and their interactions are affected in different environments is important for breeders. In the present study, quantitative trait loci mapping in a DH population of soft red winter wheat was attempted (1) to identify QTLs affecting grain yield and yield components mostly with SNP makers, (2) to determine the additive genetic effects, digenic epistasis effects and their interactions with environments.

Materials and Methods

Genetic resources

A doubled haploid (DH) population was established from the cross of the soft red winter wheat germplasm line MD01W233-06-1 (MDW233) (Costa et al., 2010) and soft red winter wheat cultivar Southern States 8641 (SS8641) (Johnson et al., 2007b). The population consists of 124 DH lines and shows a wide range of phenotypic variation for yield and yield components. MDW233 was produced by crossing the soft red winter wheat cultivar 'McCormick' (VA92–51–39 (IN71761A4–31–5-48//VA71–54–147/'McNair 1813')/AL870365 ('Coker 747*2/'Amigo')) (PI632691) (Griffey et al., 2005) with 'Choptank' ('Coker 9803'/'Freedom') (PI 639724) (Costa et al., 2006) and

was released by the Maryland Agricultural Experiment Station in 2009 with enhanced *Fusarium* Head Blight (FHB) resistance. MDW233 carries the *Rht-D1b* dwarfing gene and the *Ppd-D1b* photoperiod sensitive allele. SS8641 was photoperiod insensitive and was released by the University of Georgia Experiment Station in 2007, with high yield and multiple disease resistance (Johnson et al., 2007b). It is a medium-maturing, white-chaffed, medium-tall line derived from the cross 'GA 881130 / 2* GA 881582'. The pedigree of GA 881130 is 'KSH8998 / FR81-10 // Gore'. KSH8998 was developed from the cross of a hard wheat with *Ae. tauschii* to transfer Hessian fly resistance gene *H13*. FR81-10 was selected because of its resistance to leaf rust (*Lr37* and *Yr17*) from the cross 'Novisad 138 /4/*Ae.ventricosa*/*T.persicum*/2/ Marve*3/3/Moisson'.

Field experiments

The DH mapping population and parents were grown in five environments: Clarksville, MD and Queenstown, MD in 2013 and 2014 and at Kinston, NC in 2014. The entries were evaluated in field trials with two replications in a randomized complete block design. Yield plots at Maryland consisted of seven rows 15.2 cm apart. Seed density was 22 seeds per 0.305 m in each row. The length of rows harvested was 4.17 m, making the harvest area 3.8 m². Yield plots at North Carolina had seven rows 19.1 cm apart with a seed density of 24 seeds per 0.305 m in each row. The length of rows harvested was 3.35m, making the harvest area 3.8 m². Growing season rainfall and temperature data were obtained from respective research farms for Clarksville, MD and Queenstown, MD and the National Oceanic and Atmospheric Administration (NOAA) measurements for Kinston, NC (National Climatic Data Center 2014) (Table 2.1). Soil fertility management followed recommended management practices for each location. All trials were sprayed

with the metconazole fungicide (Caramba[®], BASF) at anthesis to reduce potential infection by *Fusarium graminearum*.

Phenotypic data collection

At maturity, plots were mechanically harvested using a small plot combine (Wintersteiger Nurserymaster Elite, Ried, Austria). Plot weight and moisture-content data of the wheat trials were obtained with a HarvestMaster HM1000b (Juniper Systems, Logan, UT) attached to the plot combine. Gain yield was measured from seed collected from the combine as pounds per plot and reported as grams per square meter. Grains per spike was recorded as the mean of the number of grains of ten random spikes from each plot. Grain weight per spike was measured using ten random spikes harvested from each plot. Spikes per square meter was calculated by dividing grain yield by grain weight per spike. Thousand-grain-weight was computed from the weight of 200 random grains from a sample harvested from each plot.

Statistical analysis of traits

Analysis of variance (ANOVA) for GYLD, GPS, GWPS, SPSM, and TGW was performed separately for each environment and for the five environments combined using the PROC GLM procedure of SAS version 9.3 (SAS Institute, Raleigh, NC 2013). The ANOVA model for single environment analysis was Y= replication + genotype + error, where replication and genotype were fixed and error was random. Combined ANOVA was performed to examine the effects of environments and the model was Y =environment + replication within environment + genotype + genotype × environment + error, where error was considered random and all others were fixed. Pearson's correlation coefficients were calculated using the PROC CORR procedure of SAS. Broad-sense heritability (h^2) (defined as $h^2 = \sigma_G^2/(\sigma_G^2 + (\sigma_{GE}^2/e) + (\sigma_E^2/re))$, where σ_G^2 is the variance of genotypic effect, σ_{GE}^2 is the genotype × environment variance, and *e* and *r* are the number of environments and replicates, respectively) was calculated on a family mean basis using the PROC MIXED procedure of SAS, as described by Holland et al. (2003). The descriptive statistics of all traits were calculated using the PROC MEANS procedure of SAS (Table 2.2).

Genotyping

SSR genotyping was performed at the USDA-ARS Eastern Regional Small Grain Genotyping Lab at Raleigh, NC, USA. Approximately 25 mg of leaf tissue of the parents and 124 doubled haploid lines were collected from 2-3 week-old seedlings for genomic DNA extraction which was performed according to the protocol of Pallotta et al. (2003). For all SSR markers, the polymerase chain reaction (PCR) master mix consisted of 2 µL of 20 ng μ L⁻¹ genomic DNA template, 0.40 μ L of a 10 μ M mixture of forward and reverse primers, 0.18 µL (0.9 U) of Tag polymerase, 1.20 µL of 10x buffer (10 mM Tris-HCL, 50 mM KCl, and 1.5 mM MgCl2, pH 8.3), 0.96 µL of a 100 µM mixture of deoxyribonucleotide triphosphates (dNTPs), and 7.26 μ L of water, bringing the total reaction volume to 12 μ L. A touchdown profile was used that consisted of an initial denaturation at 95°C followed by 15 cycles of 95°C for 45s, 65°C for 45s decreasing by 1°C each cycle, and 72°C for 60s, followed by 25 cycles of 50°C annealing temperature. The forward primers were 5'-modified to include one of the following fluorescent dyes: 6-FAM, VIC, NED, or PET. Amplifications were performed using an Eppendorf Mastercycler (Eppendorf AG, Hamburg, Germany). Sizing of PCR products was

performed by capillary electrophoresis using an ABI3130xl Genetic Analyzer (Applied BioSystems, Foster City, CA). Analysis of PCR fragments was performed using GeneMarker 1.60 software (SoftGenetics, LLC, State College, PA)

SNP genotyping was performed on the 9K iSelect SNP genotyping array containing 9,000 wheat SNP markers developed by Illumina Inc. (San Diego, CA, USA). This assay was designed under the protocols of the International Wheat SNP Consortium (Cavanagh et al., 2013). Additionally, genotyping-by-sequencing (GBS) was also employed for SNP genotyping as was described by Elshire et al. (2011). The SNP array was conducted at the USDA-ARS Small Grains Genotyping Lab at Fargo, ND, USA and GBS assay at the USDA-ARS Central Small Grain Genotyping Lab at Manhattan, KS, USA.

Map construction and QTL analysis

Markers with more than 20% missing rate and those that were monomorphic and distorted (differing significantly from the expected 1:1 segregation ratio) were eliminated from the analyses. The remaining polymorphic markers were used to construct linkage groups using the MAP function in software IciMapping version 4.0 with a LOD value of 10 (Li et al., 2008). Recombination frequencies were converted to centimorgans (cM) using the Kosambi mapping function. Assignment of linkage groups to chromosomes was based on the SNP consensus map (Cavanagh et al., 2013) and on the SSR consensus map (Somers et al., 2004), and as well as with wheat POPSEQ data (http://wheat-urgi.versailles.inra.fr/), after which, genetic distance of markers on the same chromosome was recalculated with RECORD and COUNT algorithm in IciMapping version 4.0.

Detecting QTL with additive effects was performed by IciMapping version 4.0 using the additive module (ICIM-ADD). The walking speed for all traits was 1 cM. Reference LOD values were determined by 1,000 permutations (Doerge, 2002). Type I error to determine the LOD from the permutation test was 0.05. The LOD threshold to declare the presence of a significant QTL was 3.0. The position at which the LOD score curve reaches its maximum was used as the estimate of the QTL location. Further QTL analysis for digenetic QTL epistasis (A×A or Q×Q), additive × environment (A×E or Q×E) and epistasis × environment (QQ×E) interactions was performed with QTLNetwork version 2.1 using mixed-model based composite interval mapping (MCIM) (Wang et al., 1999; Yang et al., 2007). All effects mentioned above were estimated by Monte Carlo Markov Chain method with a scanning speed of 1 cM step with a 0.05 experiment-wise type I error.

<u>Results</u>

Environment conditions

Phenotypic data for QTL analysis was collected from five environments (Table 2.1, Appendix C). The conditions at five environments varied for rainfall and average monthly temperature during each growing season. In 2013 and 2014, Queenstown had more precipitation and higher average temperature than that of Clarksville. However, both of these two locations had less precipitation and lower average monthly temperature than that at Kinston 2014. In 2013, the precipitation at Clarksville was lower than that of 2014 but the average temperature was higher implying that 2013 was a relatively warmer and drier growing season. At Queenstown, the 2013 season had more precipitation and higher average monthly temperature than that of 2014.

Environments	Precipi	tation (cm	ı)				Tempe	erature (°	C)			
	Feb.	Mar.	Apr.	May	Jun.	Total	Feb.	Mar.	Apr.	May	Jun.	Average
Queenstown 2013	6.1	9.3	11.8	4.9	24.9	57.1	2.0	5.1	12.7	17.7	23.0	12.1
Queenstown 2014	11.3	11.9	13.2	9.3	7.0	52.7	0.9	3.8	11.7	18.2	22.2	11.4
Clarksville 2013	5.0	6.5	4.7	9.0	12.7	37.9	0.6	3.8	11.8	16.5	21.9	10.9
Clarksville 2014	6.1	9.9	17.1	10.4	8.4	51.9	-1.2	2.4	10.7	17.2	22.2	10.3
Kinston 2014	6.5	14.2	11.0	8.9	26.3	67.0	8.4	9.8	17.9	22.9	25.4	16.9

Table 2.1 Growing season precipitation (cm) and average monthly temperature (°C) at five environments during 2013 and 2014.

Phenotypic performance

Analysis of variance (ANOVA) performed separately for each environment indicated significant differences (P<0.001) among all traits (data not shown). Combined ANOVA showed that genotype × environment interaction was significant (P<0.001) for GYLD, GWPS, SPSM, TGW, and GPS (Table 2.2). MDW233 had more SPSM while SS8641 had higher GPS, GWPS, and TGW across all five environments except for Clarksville 2014 where MDW233 produced slightly higher TGW than SS8641 (Table 2.2). For grain yield, MDW233 performed better in all four Maryland environments but not as well as SS8641 in Kinston 2014. Furthermore, SPSM had the most variation (measured by coefficient of variation) among all traits across five environments (Table 2.2). The DH lines showed transgressive segregation for all traits (Figure 2.1, Table 2.2). The heritability estimates were highest for thousand-grain-weight (0.92) and grain weight spike⁻¹ (0.90) followed by spikes m⁻² (0.84) and grains spike-1 (0.81), but was lowest for grain yield (0.74) (Table 2.4).

Correlation analysis (Table 2.3) showed consistently that grain yield was positively correlated with SPSM and TGW (P < 0.001). The correlation between GYLD and GPS was positive at Queenstown 2014 but was negative at Clarksville 2013 and Clarksville

2014. In general, GYLD showed the strongest positive correlation with SPSM followed by TGW. SPSM was negatively correlated with GPS and GWPS in all five environments. TGW was positively correlated with GWPS and was negatively correlated with GPS in all five environments.

DHs Parents Environments Traits **MDW233** SS8641 SD^\dagger Minimum Maximum CV^{\ddagger} Mean Clarksville 2013 GYLD 671.4 598.6 566.7 110.9 268.7 1091.6 19.6% GPS 39.9 54.8 12.9% 38.4 45.8 5.2 27.2 GWPS 1.2 1.5 1.2 0.2 0.9 1.7 15.0% SPSM 565.8 393.9 473.6 110.9 182.9 863.0 23.4% TGW 34.8 31.5 2.3 25.7 37.4 7.3% 33.4 Queenstown 2013 GYLD 712.0 664.8 736.6 144.4 363.4 1071.2 19.6% GPS 52.4 43.5 5.5 30.9 58.2 12.7% 45.7 GWPS 1.5 1.4 0.2 1.0 2.0 12.9% 1.8 951.3 SPSM 474.2 372.5 529.3 124.2 222.9 23.5% TGW 33.1 33.9 32.2 2.1 25.5 38.6 6.6% 1098.1 Clarksville 2014 GYLD 830.2 740.0 787.3 106.1 473.2 13.5% GPS 34.7 41.4 35.7 4.0 25.0 48.0 11.1% GWPS 1.0 1.3 1.0 0.1 1.4 14.3% 0.6 SPSM 794.3 572.9 806.0 160.4 490.3 1257.7 19.9% 29.4 TGW 30.7 30.3 2.5 15.8 36.6 8.4% Oueenstown 2014 GYLD 614.9 594.5 614.2 73.9 379.3 769.0 12.0% GPS 34.8 39.2 39.6 4.8 26.8 55.8 12.0% GWPS 1.0 1.2 1.1 0.1 0.8 1.5 13.0% SPSM 622.8 487.6 553.1 83.5 351.9 774.5 15.1% TGW 29.7 31.8 29.2 2.1 23.5 35.2 7.1% Kinston 2014 GYLD 615.0 679.4 555.1 92.8 228.7 837.8 16.7% GPS 35.2 46.0 42.4 5.2 32.0 59.3 12.2% GWPS 1.1 1.5 1.2 0.1 0.7 1.6 12.5% SPSM 474.6 82.7 274.9 737.9 17.4% 534.8 449.3 TGW 30.3 31.5 27.5 2.9 18.3 35.5 10.7%

Table 2.2 Phenotypic summary of grain yield (GYLD, g m⁻²), grains per spike (GPS), grain weight per spike (GWPS, g), spikes per square meter (SPSM), and thousand-grain-weight (TGW, g) evaluated in five environments during 2013 and 2014.

† Standard deviation

‡ Coefficient of variation

Environments	Traits	GPS	GWPS	SPSM	TGW
Clarksville 2013	GYLD	-0.20***	0.05	0.79***	0.33***
	GPS		0.75***	-0.62***	-0.15*
	GWPS			-0.54***	0.36***
	SPSM				0.06
Queenstown 2013	GYLD	-0.06	0.06	0.83***	0.21***
	GPS		0.82***	-0.50***	-0.22***
	GWPS			-0.48***	0.22***
	SPSM				0.09
Clarksville 2014	GYLD	-0.16***	-0.03	0.69***	0.29***
	GPS		0.64***	-0.57***	-0.24***
	GWPS			-0.70***	0.34***
	SPSM				-0.07
Queenstown 2014	GYLD	0.13*	0.22***	0.60***	0.21***
	GPS		0.77***	-0.52***	-0.30***
	GWPS			-0.62***	0.22***
	SPSM				-0.03
Kinston 2014	GYLD	-0.07	0.33***	0.74***	0.44***
	GPS		0.61***	-0.49***	-0.39***
	GWPS			-0.36***	0.36***
	SPSM				0.17**

Table 2.3 Pearson correlation coefficients among grain yield (GYLD), grains per spike (GPS), grain weight per spike (GWPS), spikes per square meter (SPSM), and thousand-grain-weight (TGW) in five environments during 2013 and 2014.

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level. *** Significant at the 0.001 probability level.

Table 2.4 Pooled analyses of variance over five environments and heritability estimates for grain yield (GYLD), grains per spike (GPS), grain weight per spike (GWPS), spikes per square meter (SPSM), and thousand-grain-weight (TGW) in five environments during 2013 and 2014.

		Mean squares				
Source of Variation	df	GYLD	GPS	GWPS	SPSM	TGW
Environment	4	2697855.85*	2260.17*	5.64*	4679695.46*	841.21*
Rep (environment)	5	100996.06*	179.67*	0.45*	429149.39*	8.00*
Genotype	123	40596.54*	136.50*	0.11*	47696.44*	38.96*
Genotype × environment	492	10475.85*	13.18*	0.02*	8954.60*	3.29*
\mathbb{R}^2		0.85	0.85	0.86	0.88	0.95
Heritability $(h^2)^{\dagger}$		0.74 (0.04)	0.81 (0.03)	0.90 (0.01)	0.84 (0.02)	0.92 (0.01)

* Significant at the 0.001 probability level.

† Values in parenthesis are standard errors for h^2

Linkage map construction

The DH population was analyzed with 4981 markers that were polymorphic between the two parents (4956 SNPs, 24 SSRs and 1 morphological marker). A total of 4972 markers (99.8%) were assigned to 39 linkage groups representing all 21 wheat chromosomes (Table 2.5). After excluding co-segregating markers, the final genetic linkage map was constructed with 859 unique makers that spanned 1977.62 cM in length (Appendix A). The average interval length was 2.3 cM. Since the recommended map distance for QTL analysis is ten re-combinations per 100 meiotic events, or an interval length less than 10 cM (Doerge, 2002), the map is suitable for QTL analysis in this study.

Chromosome	Number of markers	Length (cM)
1A	521	67.71
2A	298	112.3
3A	333	216.84
4A	272	158.28
5A	218	190.04
6A	242	95.05
7A	365	171.5
1B	257	144.13
2B	516	139.83
3B	488	134
4B	121	134.51
5B	430	123.21
6B	286	112.39
7B	245	177.83
1D	55	85.55
2D	116	125.93
3D	29	72.74
4D	8	76.77
5D	36	179.45
6D	81	144.64
7D	55	259.8

Table 2.5 Distribution of markers and length of linkage maps for twenty one wheat chromosomes.

Table 2.6 Quantitative trait loci (QTLs), LOD score, percentage of variation explained (PVE), and additive effects of each QTL for grain yield (GYLD, g m⁻²), grains per spike (GPS), grain weight per spike (GWPS, g), spikes per square meter (SPSM), and thousand-grain-weight (TGW, g) in five environments during 2013 and 2014.

QTL	Trait	Environment	Position (cM)	Marker interval	LOD score	PVE (%)	Additive effect
Qyld.cz-1A	GYLD	Clarksville 2013	0	Xwmc496-Xsnp1970	3.4128	7.4686	-25.6006
Qyld.cz-2A	GYLD	Kinston 2014	0	Xsnp2477-Xsnp2432	4.2968	9.9008	25.211
Qyld.cz-3A	GYLD	Clarksville 2014	0	Xsnp3027-Xsnp3744	3.0403	8.6136	-24.2575
Qyld.cz-6A	GYLD	Queenstown2014	75	Xsnp4211-Xsnp4186	3.455	9.7424	19.1153
Qyld.cz-1B	GYLD	Clarksville 2013	74	Xsnp4928-Xsnp2107	5.6376	13.2401	-35.0708
Qyld.cz-3B.1	GYLD	Kinston 2014	7	Xbarc147-Xsnp3328	4.5878	10.9125	-26.2832
Qyld.cz-3B.2	GYLD	Clarksville 2014	60	Xsnp3382-Xsnp3372	6.7965	21.2499	-38.2413
Qyld.cz-5B.1	GYLD	Clarksville 2013	66	Xsnp4059-Xsnp4061	5.5119	12.7278	-33.4221
Qyld.cz-5B.2	GYLD	Kinston 2014	115	Xsnp4011-Xsnp4073	4.4601	10.2934	25.6696
Qyld.cz-6B	GYLD	Kinston 2014	6	Xsnp4444-Xsnp4453	4.6423	10.9935	26.3474
Qyld.cz-2D	GYLD	Queenstown2013	54	Xsnp2862-XPpdD1	4.5148	17.7026	52.6542
Qyld.cz-6D	GYLD	Clarksville 2013	137	Xsnp4465-Xsnp4487	6.677	15.5547	-37.1149
QGps.cz-1A.1	GPS	Kinston 2014	1	Xsnp1970-Xbarc28	14.2219	26.511	2.439
QGps.cz-1A.2	GPS	Clarksville 2013	2	Xbarc28-Xsnp2005	21.1713	44.118	2.9461
QGps.cz-1A.2	GPS	Clarksville 2014	2	Xbarc28-Xsnp2005	11.0378	22.5923	1.6195
QGps.cz-1A.2	GPS	Queenstown2013	2	Xbarc28-Xsnp2005	12.5949	29.3932	2.681
QGps.cz-1A.2	GPS	Queenstown2014	2	Xbarc28-Xsnp2005	8.5734	18.1522	1.7105
QGps.cz-2A	GPS	Queenstown2014	40	Xsnp2448-Xsnp2475	4.6006	8.99	-1.2111
QGps.cz-3A.1	GPS	Kinston 2014	2	Xsnp3048-Xsnp1466	4.4227	6.9464	1.2484
QGps.cz-3A.2	GPS	Clarksville 2013	5	Xsnp3049-Xsnp3021	24.1227	51.9916	-3.1986
QGps.cz-3A.3	GPS	Clarksville 2013	124	Xsnp3037-Xsnp3023	5.1633	8.0188	1.264
QGps.cz-3A.4	GPS	Clarksville 2014	126	Xsnp3023-Xsnp3383	3.4903	6.0965	0.8454
QGps.cz-3A.4	GPS	Kinston 2014	126	Xsnp3023-Xsnp3383	5.269	8.2402	1.3662
QGps.cz-4A	GPS	Queenstown2014	138	Xsnp3464-Xsnp3547	3.2552	6.2726	1.0236
QGps.cz-2B	GPS	Queenstown2013	62	Xsnp2752-Xsnp2786	3.9483	7.8456	-1.3878
QGps.cz-3B.1	GPS	Kinston 2014	34	Xsnp3344-Xsnp3253	6.3159	10.277	1.5188
QGps.cz-3B.2	GPS	Queenstown2013	36	Xsnp3253-Xsnp3349	4.5431	9.3033	1.5085
QGps.cz-3B.3	GPS	Clarksville 2014	47	Xsnp3119-Xsnp3395	7.0831	13.3475	1.2462
QGps.cz-5B.1	GPS	Clarksville 2013	45	Xsnp3973-Xsnp4062	4.5948	6.7766	-1.1547
QGps.cz-5B.2	GPS	Queenstown2014	48	Xsnp4083-Xsnp3988	7.6516	15.9459	-1.6031
QGps.cz-5B.3	GPS	Clarksville 2014	58	Xsnp3988-Xsnp1006	5.6091	10.3121	-1.0956
QGps.cz-5B.4	GPS	Kinston 2014	68	Xsnp4061-Xsnp4027	6.9909	11.3158	-1.5936
QGps.cz-3D	GPS	Queenstown2014	72	Xsnp3422-Xsnp3187	3.8018	7.4961	-1.1211
QGws.cz-1A.1	GWPS	Clarksville 2013	0	Xwmc496-Xsnp1970	12.1722	28.5671	0.079
QGws.cz-1A.2	GWPS	Clarksville 2014	1	Xsnp1970-Xbarc28	11.5142	33.1833	0.0641
QGws.cz-1A.2	GWPS	Kinston 2014	1	Xsnp1970-Xbarc28	7.284	20.32	0.0599
QGws.cz-1A.2	GWPS	Queenstown2013	1	Xsnp1970-Xbarc28	11.28	32.2485	0.0937
QGws.cz-1A.3	GWPS	Queenstown2014	2	Xbarc28-Xsnp2005	5.0104	15.4379	0.0446
QGws.cz-3A	GWPS	Clarksville 2014	188	Xsnp2984-Xsnp2934	3.1047	7.4815	-0.0306
QGws.cz-5A	GWPS	Clarksville 2013	87	Xsnp3843-Xsnp3820	4.6284	9.4469	0.046
QGws.cz-5B	GWPS	Clarksville 2013	20	Xsnp4130-Xsnp3884	3.602	7.2761	-0.0398
QGws.cz-6B	GWPS	Kinston 2014	63	Xsnp4421-Xsnp4451	4.8634	13.2328	0.0483
QGws.cz-7B	GWPS	Clarksville 2014	58	Xsnp4927-Xsnp489	3.1066	7.472	0.0305

Table 2.6 Continued

QTL	Trait	Environment	Position (cM)	Marker interval	LOD score	PVE (%)	Additi effe
QSsm.cz-1A.1	SPSM	Clarksville 2013	0	Xwmc496-Xsnp1970	13.8851	30.1443	-50.84
QSsm.cz-1A.1	SPSM	Clarksville 2014	0	Xwmc496-Xsnp1970	4.434	10.2247	-35.31
QSsm.cz-1A.2	SPSM	Kinston 2014	1	Xsnp1970-Xbarc28	15.5894	22.0811	-34.03
QSsm.cz-1A.3	SPSM	Queenstown2013	3	Xbarc28-Xsnp2005	8.2625	22.9784	-51.55
QSsm.cz-1A.3	SPSM	Queenstown2014	2	Xbarc28-Xsnp2005	6.9139	15.2758	-25.08
QSsm.cz-2A.1	SPSM	Kinston 2014	0	Xsnp2477-Xsnp2432	3.3285	3.7029	14.05
QSsm.cz-2A.2	SPSM	Queenstown2014	75	Xsnp2382-Xsnp2401	4.8376	10.2491	20.70
QSsm.cz-3A	SPSM	Kinston 2014	1	Xsnp3744-Xsnp3048	3.5396	3.9658	-14.43
QSsm.cz-6A	SPSM	Clarksville 2014	81	Xsnp4197-Xsnp473	3.6434	8.2722	31.94
QSsm.cz-1B.1	SPSM	Kinston 2014	8	Xsnp2205-Xsnp4503	3.241	3.6256	-13.8
QSsm.cz-1B.2	SPSM	Clarksville 2013	72	Xsnp4928-Xsnp2107	3.362	6.142	-23.3
QSsm.cz-3B.1	SPSM	Queenstown2014	24	Xsnp3405-Xsnp3389	5.7956	12.7812	-23.02
QSsm.cz-3B.2	SPSM	Kinston 2014	31	Xsnp3389-Xsnp3344	5.9097	6.9082	-19.07
QSsm.cz-3B.3	SPSM	Clarksville 2014	46	Xsnp3335-Xsnp3119	3.8828	8.9779	-33.13
QSsm.cz-3B.4	SPSM	Kinston 2014	129	Xsnp3401-Xsnp3358	3.3933	3.8222	-14.20
QSsm.cz-5B.1	SPSM	Clarksville 2013	75	Xsnp4072-Xsnp4085	3.1264	5.6471	-22.02
QSsm.cz-5B.2	SPSM	Kinston 2014	116	Xsnp4011-Xsnp4073	5.1611	6.03	17.93
QSsm.cz-6B	SPSM	Kinston 2014	3	Xsnp4456-Xsnp107	10.2874	13.4102	26.53
QSsm.cz-2D	SPSM	Queenstown2013	57	Xsnp2862-XPpdD1	4.7473	12.6431	38.58
QSsm.cz-3D	SPSM	Queenstown2014	57	Xsnp3422-Xsnp3187	4.858	10.5722	21.19
QSsm.cz-6D	SPSM	Clarksville 2013	137	Xsnp4465-Xsnp4487	3.2886	5.8034	-22.4
QTgw.cz-3A.1	TGW	Clarksville 2013	126	Xsnp3023-Xsnp3383	5.3262	8.2592	-0.63
QTgw.cz-3A.2	TGW	Queenstown2013	136	Xsnp1758-Xsnp1485	6.4554	11.2965	-0.69
QTgw.cz-3A.3	TGW	Queenstown2014	137	Xsnp1485-Xsnp2964	4.5797	9.3414	-0.60
QTgw.cz-3A.4	TGW	Clarksville 2014	143	Xsnp2885-Xsnp2987	3.0018	4.914	-0.5
QTgw.cz-3A.5	TGW	Kinston 2014	147	Xsnp2937-Xsnp4728	4.9325	12.6304	-1.00
QTgw.cz-3A.6	TGW	Clarksville 2013	208	Xsnp2951-Xsnp2971	4.2346	6.7403	-0.5
QTgw.cz-5A.1	TGW	Kinston 2014	53	Xsnp218-Xsnp49	3.5745	8.8337	0.84
QTgw.cz-5A.2	TGW	Clarksville 2013	58	Xsnp3838-Xbarc100	7.3695	11.6843	0.70
QTgw.cz-5A.3	TGW	Clarksville 2014	60	Xbarc100-Xsnp4843	5.4004	9.237	0.7
QTgw.cz-5A.3	TGW	Queenstown2013	61	Xbarc100-Xsnp4843	5.7471	10.1805	0.6
QTgw.cz-7A.1	TGW	Queenstown2013	18	Xsnp4718-Xsnp4759	4.8786	8.2581	-0.59
QTgw.cz-7A.2	TGW	Clarksville 2013	105	Xsnp4637-Xsnp4567	5.1786	8.0243	0.62
QTgw.cz-7A.3	TGW	Queenstown2014	107	Xsnp4946-Xsnp4546	6.7631	14.7144	0.76
QTgw.cz-7A.4	TGW	Clarksville 2014	115	Xsnp4935-Xsnp4622	5.7396	9.8599	0.73
QTgw.cz-7A.5	TGW	Queenstown2013	123	Xsnp4588-Xsnp4620	26.7529	71.1913	-1.76
QTgw.cz-1B.1	TGW	Clarksville 2013	85	Xsnp2084-Xsnp2113	6.3088	9.8591	-0.69
QTgw.cz-1B.1	TGW	Clarksville 2014	86	Xsnp2084-Xsnp2113	3.6645	6.0751	-0.57
QTgw.cz-1B.2	TGW	Queenstown2014	87	Xsnp2113-Xsnp2091	3.6309	7.2769	-0.54
QTgw.cz-2B	TGW	Clarksville 2014	58	Xbarc10-Xsnp2744	6.1855	10.8214	0.76
QTgw.cz-2B	TGW	Kinston 2014	58	Xbarc10-Xsnp2744	4.7936	12.1618	0.98
QTgw.cz-4B	TGW	Queenstown2013	75	Xsnp3721-Xsnp1656	4.2407	7.1261	0.50
QTgw.cz-7B.1	TGW	Clarksville 2014	58	Xsnp4927-Xsnp489	5.7036	10.3833	0.5
QTgw.cz-7B.1	TGW	Queenstown2013	58	Xsnp4927-Xsnp489	3.0727	5.3189	0.4
QTgw.cz-7B.2	TGW	Clarksville 2013	63	Xsnp838-Xsnp4852	7.3537	11.8238	0.75
QTgw.cz-7B.3	TGW	Queenstown2014	65	Xsnp4852-Xsnp4943	4.2808	9.5333	0.61
QTgw.cz-5D	TGW	Clarksville 2013	95	Xsnp4052 Xsnp4045 Xsnp4170-Xsnp4157	3.6356	5.4776	0.51

QTL with additive and additive × environment interaction effects

ICIM-ADD mapping detected a total of 64 putative QTLs for grain yield and yield components at five environments (Table 2.6). Significant QTLs were detected on all chromosomes except 1D, 4D, and 7D. QTLs were unevenly distributed across the three homoeologous groups and twenty one chromosomes of wheat. Thirty QTLs (46.9%) were in the A genome, also 30 QTLs (46.9%) were in the B genome, and only 4 (6.3%) were in the D genome. Distribution of QTLs was also unbalanced on chromosomes among homologous chromosome groups as follows: 7 on chromosomes 1 (11.1%), 6 on chromosomes 2 (9.4%), 22 on chromosomes 3 (34.4%), 2 on chromosomes 4 (3.1%), 13 on chromosomes 5 (20.3%), 6 on chromosomes 6 (9.4%), and 8 on chromosomes 7 (12.5%).

The number of QTL for individual traits ranged from 8 to 22. Specifically, 12 QTL were identified for grain yield and each of them explained 7.5% to 21.3% of the phenotypic variation; 17 QTL were identified for grains spike⁻¹ explaining 6.1 % to 44.1% of the phenotypic variation; 19 QTL were detected for spikes m⁻² and 8 QTL were for grain weight spike⁻¹ accounting for 3.7% to 15.6% and 7.3% to 33.2% of the phenotypic variation respectively; 22 significant QTL were found to explain 5.5% to 71.2% of the phenotypic variation of thousand grain weight. In addition, 11 marker intervals where QTL co-location existed were estimated to have pleiotropic effects. Among all QTL identified, 6 QTL were repeatedly detected in more than one environment.

Additive × environment interaction effects were detected for all traits evaluated except for TGW. Of the five significant QTLs, three were detected with additive main effects in previous single environment mapping and the other two were insignificant (LOD<3) for additive main effects, hence, were environment-specific QTLss (Table 2.7). The heritability of additive × environment interactions ranged from 0.2% to 27.4%. Clarksville 2013 had the most additive × environment interactions, followed by Queenstown 2014. One additive × environment interaction was detected for Clarksville 2014 and Kinston 2014 and none were detected for Clarksville 2013.

QTL with epistatic and epistasis × environment interaction effects

A total of 7 pairs of significant epistatic interactions (P < 0.001) were identified across five environments for yield and yield components except for SPSM (Table 2.8). The epistatic interactions were observed within and across chromosomes (mostly in the A and B genome) with heritability ranging from 0.2% to 6% and 0.1% to 2.7% for epistatic and epistatic × environment interaction effects, respectively. The only significant epistatic × environment interaction identified in this study was in Queenstown 2013. Furthermore, two marker intervals *Xbarc28-Xsnp2005* and *Xsnp3253-Xsnp3349*, had already been detected for significant additive effects (Table 2.6) while the rest were detected only for epistatic interactions.

Q <mark>g</mark> ws.cz-1A. Qgws.cz-1A.	Q.Ssm.cz-1A.2 Q.Ssm.cz-1A.2 Q.Ssm.cz-1A.1 Q.G.ws.cz-1A.3	q Yld.cz-1A	3A 0.0 Xsnp: 0.9 Xsnp: 1.8 Xsnp: 3.6 Xsnp: Xsnp: Xsnp: Xsnp: Xsnp:	3744 9	QGps.cz-3A.2	QSsm.cz-3A			QYId.cz-3A
2-1A.2 2A	27A.3 27A.2 27A.1 27A.3	1 1 2 2 2 2 3 3 3 3 3 3 3 3 3 3 3 3 3 3	1.0 Xsnp Xsnp Xsnp	12 3008 2993 1522 3034 3051 3046 3064 3040 3094 3056	z-3A.2	z-3A			-3A
-ff-	Xsnp2477 -O Xsnp2432 S		9.1	2988					
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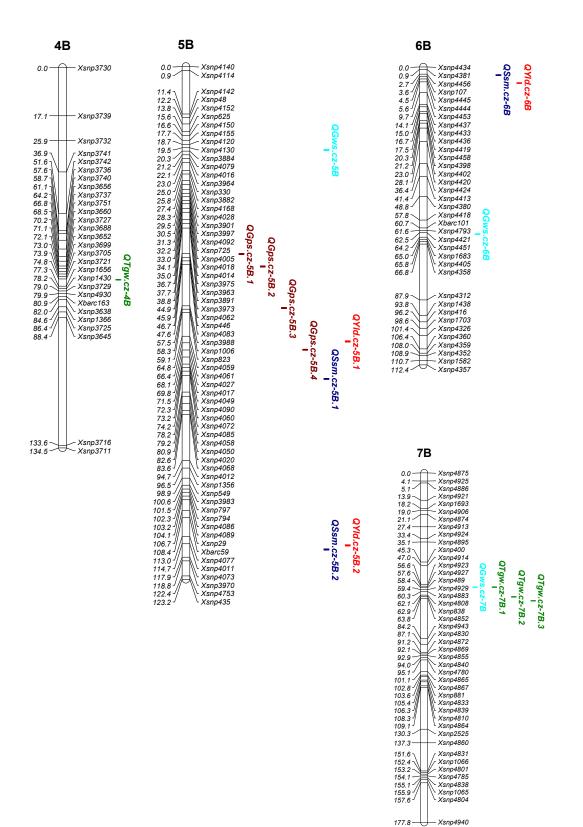
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33.8 / Xsnp767 Xsnp2130 Xsnp2073 49.2 / Xsnp2073 50.0 / Xsnp2110 50.0 / Xsnp854 Xsnp2121 52.7 / Xsnp2053 Xsnp2053 Xsnp2092 59.7 / Xsnp2064 61.4 / Xsnp2117 64.0 / Xsnp2117 64.0 / Xsnp2117 65.8 / Xsnp2117	34.5 36.2 46.4 47.3 58.3 59.1 60.0 61.1 62.2 63.2 7.5snp2769 7.barc10 7.snp2709 7.barc10 7.snp2709 7.barc10 7.snp2705 7.snp2705 7.snp2705 7.snp2774 7.snp27752 7.snp2776 7.snp2775 7.snp2776 7.snp2775 7.snp2776 7.snp2778 7.snp2768 7.snp2778 7.snp2768 7.snp2778 7.snp2768 7.snp2778 7.snp2768 7.snp2778 7.snp2768 7.snp2778 7.snp2768 7.snp2778 7.snp2768 7.snp2778 7.snp2768 7.snp2768 7.snp2768 7.snp2768 7.snp2768 7.snp2778 7.snp2768 7.snp2768 7.snp2767 7.snp2569 7.snp25	22.4 Xsnp3288 Xsnp3405 Xsnp3340 31.0 Xsnp3344 35.3 Xsnp3323 41.8 Xsnp3347 42.7 Xsnp3367 43.5 Xsnp3320 44.3 Xsnp33367 Xsnp3320 44.3 Xsnp33367 Xsnp3320 45.3 Xsnp3347 Xsnp3347 Xsnp3319 47.3 Xsnp3347 Xsnp3347 Xsnp3319 47.3 Xsnp3319 47.3 Xsnp3347 Xsnp3319 47.3 Xsnp3319 47.3 Xsnp3319 47.3 Xsnp3319 Xsnp3357 Xsnp357 X	QSsm.cz-3B. 2-3B.2 QGps.cz-3B ps.cz-3B.2
67.7 68.6 67.2 71.2 72.1 74.1 75.1 86.3 87.3 87.3 87.3 87.9 17.4 Xsnp2126 Xsnp4928 Xsnp2126 Xsnp2106 Xsnp2106 Xsnp2005 Xsnp205 17.7 Xsnp2052	18.2 0.9.0 70.9 73.8 73.87 73.87 73.872569 73.8725666 73.8725666	 53.2 55.1 55.1 56.7 57.6 60.9 61.9 62.7 63.6 64.5 66.2 67.1 58.67 59.7 50.7 <l< td=""><td>9Yld.cz-3B.2 3 .3</td></l<>	9Yld.cz-3B.2 3 .3
124.8 Xsnp2059 125.6 Xsnp2111 128.9 Xsnp2116 133.2 Xsnp2067 141.7 Xsnp2127 144.1 Xsnp2127	90.0 Xsnp2515 90.8 Xsnp2176 92.5 Xsnp2644 93.5 Xsnp2648 94.5 Xsnp2615 95.5 Xsnp2619 98.3 Xsnp2619 100.2 Xsnp2523 102.1 Xsnp265 103.8 Xsnp2665 105.8 Xsnp2665 105.8 Xsnp2649 105.9 Xsnp2649 115.9 Xsnp2585 116.8 Xsnp281	72.5 Xsnp3410 73.4 Xsnp3416 74.3 Xsnp3416 75.4 Xsnp3346 75.4 Xsnp3347 76.2 Xsnp31697 80.4 Xsnp31697 81.3 Xsnp3112 85.6 Xsnp33112 87.3 Xsnp3345 93.9 Ssnp3345 97.3 Xsnp3174 98.1 Ysnp3174 101.5 Xsnp3174	٥
	119.4 Xsnp22666 122.1 Xsnp2574 123.7 Xsnp2574 125.4 Xsnp2603 130.3 Xsnp2586 133.9 Xsnp2600 134.8 Xsnp2579 137.1 Xsnp26079 138.0 Xsnp2802 139.0 Xsnp2496 139.8 Xsnp2663	107.2 109.0 128.2 130.0 130.0 130.0 131.8 132.8 134.0 Xsnp3418 Xsnp3418 Xsnp34175 Xsnp3407 Xsnp3400 Xsnp3406 Xsnp3403 Xsnp3403 Xsnp3181	QSsm.cz-3B.4



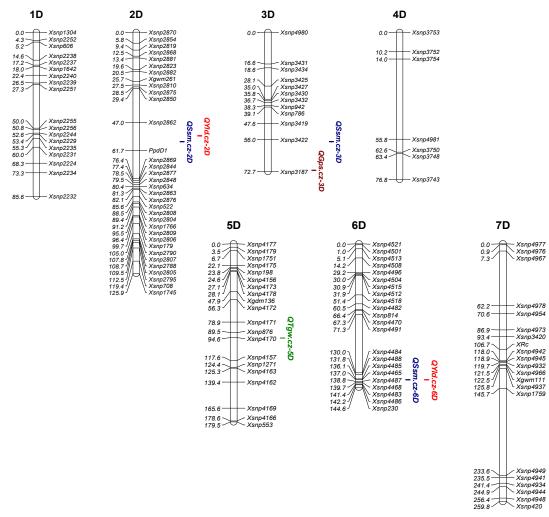


Figure 2.1 Genetic linkage map and position of quantitative trait loci (QTLs) detected in a doubled haploid mapping population derived from MD01W233-06-1 × SS8641. Locus marker names are shown on the right side of the chromosomes and values to the left of chromosomes show the genetic distance (cM) for each marker. QTLs are labeled with trait abbreviations and the QTL number for each trait. QTLs for the same trait are in the same color.

Table 2.7 QTL × Environment interactions influencing grain yield (GYLD), grains per spike (GPS), grain weight per spike (GWPS), spikes per square meter (SPSM), and thousand-grain-weight (TGW) in five environments during 2013 and 2014.

Trait	Chr.	Position	Interval	AE1 [†]	AE2 [†]	AE3 [†]	$AE4^{\dagger}$	AE5 [†]	h ²(ae) ‡
GYLD	2A	23.6	Xsnp2427-Xsnp2479			-15.27*		12.78*	0.002
GYLD	2A	88.8	Xsnp2406-Xsnp2363			19.00**			0.030
GPS	1A	3.7	Xbarc28-Xsnp2005§			0.52*	-0.66**		0.274
SPSM	1A	1.7	Xbarc28-Xsnp2005§				12.87*		0.217
SPSM	3B	46.2	Xsnp3119-Xsnp3395§		-14.30*				0.099

† AE is the additive × environment interaction effect at each environment. E1: Clarksville 2013; E2: Clarksville 2014; E3: Queenstown 2013; E4: Queenstown 2014; E5: Kinston 2014.

 $\frac{1}{8}h^2$ (ae) is heritability estimate of the additive × environment interaction effect across five environments. Interval with significant additive effect.

* Significantly different from zero at the 0.05 probability level.

** Significant difference from zero at the 0.01 probability level.

Table 2.8 Chromosome locations of digenetic epistatic QTLs for grain yield (GYLD), grains per spike (GPS), grain weight per spike (GWPS), spikes per square meter (SPSM), and thousand-grain-weight (TGW) in five environments in 2013 and 2014.

Trait	Interval ⁺	Chr^{\dagger}	Position ⁺	Interval [‡]	Chr [‡]	Position [‡]	AA§	E1¶	E2¶	E3 ¶	E4¶	E5¶	h²(aa) #	h²(aae) **
GYLD	Xsnp4749-Xsnp324	7A	53.6	Xsnp3312-Xsnp1697	3B	76.2				23.79***			0.2%	2.7%
GYLD	Xsnp4171-Xsnp876	5D	83.9	Xsnp4518-Xsnp4482	6D	56.4	17.11***						2.5%	0.9%
GPS	Xbarc28-Xsnp2005 ^{‡‡}	1A	3.7	Xsnp1006-Xsnp823	5B	58.3	-0.50***						1.5%	0.5%
GPS	Xsnp4715-Xsnp4722	7A	49.3	Xsnp2780-Xsnp3734	2B	17.3	-0.46***						1.5%	0.6%
GWPS	Xsnp2956-Xsnp2950	3A	155.9	Xsnp2571-Xsnp2667	2B	86.4	0.03***						3.5%	0.9%
TGW	Xsnp4050-Xsnp4020	5B	80.9	Xsnp4451-Xsnp1683	6B	64.2	0.29***						3.1%	0.1%
TGW	Xsnp3253-Xsnp3349 ^{‡‡}	3B	35.3	Xsnp3175-Xsnp3401	3B	120	0.65***						6.0%	0.1%
TGW	Xsnp3645-Xsnp3716	4B	114.4	Xsnp4948-Xsnp420	7D	256.4	-0.58***						4.3%	0.1%

[†] The flanking markers, chromosome and position of the first interval involved in the epistasis.

‡ The flanking markers, chromosome and position of the second interval involved in the epistasis.

§ The additive × additive effect.

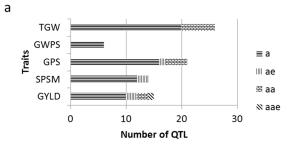
¶ The epistasis × environment effect at each environment. E1: Clarksville 2013; E2: Clarksville 2014; E3: Queenstown 2013; E4: Queenstown 2014; E5: Kinston 2015.

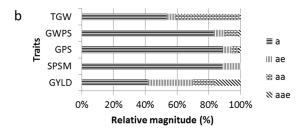
The heritability estimates for additive × additive interaction effects across five environment.

^{††} The heritability estimates for epistasis × environment interaction effects across five environments.

‡[‡] Interval with significant additive effect.

*** Significantly different from zero at the 0.001 probability level.





►

Figure 2.2 Distribution of genetic and non-genetic components for grain yield and yield related traits: grain yield (GYLD), spikes m^{-2} (SPSM), grains per spike (GPS), grain weight per spike (GWPS), thousand-grain-weight (TGW). a) total number of QTLs detected for additive (*a*), additive × environment (*ae*), epistasis (*aa*), and epistasis × environment interactions (*aae*) effects. b) relative magnitude of *a*, *ae*, *aa*, and *aae* effects.

Discussion

Grain yield and yield components are complex quantitative traits determined by genetic components, environmental factors, and the interaction between them (Cooper et al., 2009; Eeuwijk, 2008; Holland, 2007; Mackay, 2001). In this study, I used a mixed linear model to investigate the genetic basis of grain yield and yield components in a DH population of 124 lines by dividing genetic effects into additive main effect (A), additive \times additive epistatic main effects (A \times A or Q \times Q), and their environmental interaction effects (A×E, AA×E or Q×E, QQ×E) (Wang et al., 1999; Yang et al., 2007). As single environment experiment could underestimate the number of QTL controlling a certain trait, whereas repeated experiments are useful in detecting stable QTL over environments (Paterson et al., 1991), I evaluated the DH population and parents in five environments in the US East Coast. For genotyping, I relied mostly on SNPs by using the 9K SNP array and GBS in addition to SSRs to get more coverage of the wheat genome. The map contained 4972 polymorphic markers and is highly consistent with the previously published 9K SNP consensus map (Cavanagh et al., 2013). The rank correlation coefficient between them was as high as 0.99 for most chromosomes in terms of SNP order (data not shown). Furthermore, the average interval length of the map (2.3 cM) was much smaller than that observed in previous studies (Carter et al., 2011; Heidari et al., 2011; Li et al., 2013), indicating a better resolution.

QTLs for grain yield

In this study, grain yield was defined as yield m^{-2} as reported by previous researchers (Heidari et al., 2011; Lopes et al., 2013). Twelve grain yield QTLs were detected (Table 2.6). Both parents carried favorable QTL alleles. Seven loci of MDW233 alleles increased grain yield on 1A, 3A, 3B, 5B, 6D, accounting for 7.5 to 21.3% of the phenotypic variation. The SS8641 alleles were associated greater grain yield at the other five loci on 2A, 6A, 5B, 6B, 2D, accounting for 9.7 to 17.7% of the phenotypic variation. Grain yield was the only trait that had no stable QTL detected over five environments in this study. This was expected as similar results were obtained by Kumar et al. (2007) and Li et al. (2007b), verifying that grain yield is strongly influenced by environment. Furthermore, QTL is a genomic region that may contain several functional genes or sub-QTLs that are closely linked and may have opposite genetic effects and as well as being subject to environmental influences (Mackay et al., 2009). The detection of a QTL indicates that the net effects of all sub-QTLs within it are significant whereas a non-significant QTL may still contain significant sub-QTLs (Mackay et al., 2009). Therefore, increasing marker density and population size would allow for the discovery of more QTLs as well as develop more detailed insights into the genetic basis of quantitative traits in this DH population.

Eight QTL (*QYld.cz-1B, QYld.cz-3B.1, QYld.cz-3B.2, QYld.cz-5B.1, QYld.cz-5B.2, QYld.cz-6B, QYld.cz-2D, QYld.cz-6D*) explained more than 10 % of the phenotypic variation of grain yield (Table 2.6). The QTL *QYld.cz-3B.2* was detected at

Clarksville 2014 with LOD=6.8 and the effect of MDW233 allele was very large accounting for the highest genetic variation for gain yield (PVE=21.3%). In this region, Bennett et al. (2012a) and Bennett et al. (2012b) also reported QTLs for grain yield, spike length, thousand grain weight repeatedly in heat, drought and high yield potential environments and Zhang et al. (2010) identified two meta-QTLs for grain yield and yield associated traits in a meta-QTL analysis based on 59 independent studies. Other studies also identified QTLs for plant height, harvest index, isotope discrimination, and canopy temperature in this region (Bennett et al., 2012b; Cuthbert et al., 2008; Kumar et al., 2007; Rebetzke et al., 2008). To date, the region where *QYId.cz-3B.2* resides appears to have pleiotropic effect on grain yield and should be given high priority for fine mapping and candidate gene identification, so that diagnostic gene-specific markers can be developed and utilized within breeding programs.

QYld.cz-2D (LOD=4.5148, PVE=17.7%) was flanked by *Xsnp2862* and *Ppd-D1*. *Ppd-D1* is a photoperiod-sensitivity gene that largely confers wheat dominant insensitivity to short day length. It enhances grain yield by allowing earlier heading under the short days of spring so that grain-filling can occur before heat and drought stress often associated with late summer (Nelson et al., 2006). Moreover, a recent study showed that *Ppd-D1* controlled photoperiod dependent floral induction in wheat and had a major inhibitory effect on paired spikelet formation by regulating the expression of *FLOWERING LOCUS T* (*FT*) (Boden et al., 2015). The yieldincreasing effect of *QYld.cz-2D* may be due to the pleiotropic effect of *Ppd-D1*.

OYld.cz-3B.1 (LOD=4.6, PVE=10.9%) was mapped on the short arm of chromosome 3B and may be related to the one detected by Li et al. (2007b). Another well-known QTL, Ofhs.ndsu-3BS (also known as resistance gene Fhb1), is located in the same region (Schweiger et al., 2013). This suggests a possible new way to improve wheat disease resistance and grain yield by deploying this genomic region in breeding lines. Additionally, QTL QYld.cz-1A was in a region similar to that identified by Heidari et al. (2011) which controlled the expression of both grains per spike and grain weight per spike. Previous studies also detected QTL for grain yield in similar regions for OYld.cz-3A (Campbell et al., 2003; Mengistu et al., 2012), OYld.cz-1B (Huang et al., 2003), OYld.cz-5B.1 (Bennett et al., 2012b), OYld.cz-6A (Kuchel et al., 2007b; Simmonds et al., 2014), QYld.cz-6B (Marza et al., 2006), and QYld.cz-6D (Kumar et al., 2007). Yield QTLs reported by Kumar et al. (2007) and Groos et al. (2003) were located in a region more than 10 cM away from OYld.cz-2A and OYld.cz-5B.2, respectively. This suggests that *OYld.cz-2A* and *OYld.cz-5B.2* may be new QTLs or this could be due to the difference in linkage map resolution.

QTLs for yield components

In this study, TGW had the highest heritability and number of QTLs among all traits evaluated (Table 2.4 and 2.6). Of the twenty-two QTLs identified, four were detected in more than one environment. They were located on chromosomes 5A, 1B, 2B, and 7B. However, the strongest QTL was on chromosome 7A, designated as *QTgw.cz-7A.5*, and explained up to 71.2% of the variation of TGW in Queenstown 2013. The positive allele for this QTL was from MDW233, the parental line with the lower

TGW. Similarly, Groos et al. (2003) also reported a stable QTL in this region for TGW explaining 5.2 to 10.3% of the phenotypic variation across seven trials. Thus, OTgw-7A.5 may be the underlying QTL in both studies. Four QTL clusters were found on 3A, 1B, 5A and 7B as QTLs on those chromosomes were detected in proximity to each other and exhibited the same direction of genetic effects (Cai and Morishima, 2002). Specifically, favorable allelic clusters on 3A and 1B came from MDW233 while those alleles from SS8641 were associated with higher TGW for the allelic clusters on 5A and 7B. Extensive studies have focused on 3A, which is known to contain QTL/genes controlling grain yield and associated traits, and several loci for TGW were identified (Dilbirligi et al., 2006; Mengistu et al., 2012; Rustgi et al., 2013). However, after a close comparison of previous results, I found that *QTgw.cz*-3A.6 appeared to be a new QTL for TGW since no TGW QTLs were reported in this region before. Clusters/QTL have also been reported in similar regions for the ones on 3A (Huang et al., 2004), 5A (Cuthbert et al., 2008), 7B (Hai et al., 2008; Huang et al., 2003),1B (Huang et al., 2004), QTgw.cz-2B (Hai et al., 2008), QTgw.cz-5D (Li et al., 2007b).

QTLs for GPS have been identified on all wheat chromosomes (Tang et al., 2011; Wu et al., 2012; Zhang et al., 2010). In the present study, several major GPS QTLs on 1A, 3A and 5B were detected and formed QTL clusters. The QTL cluster on 1A was detected in all five environments and explained 18.2 to 44% of the phenotypic variation. Heidari et al. (2011) found the same region significantly associated with GPS but with less PVE. The QTL cluster (*QGps.cz-3A.1* and *QGps.cz-3A.2*) at the

distal end short arm of 3A is comparable with the region identified for GPS, GYLD, and TGW by Campbell et al. (2003). *QGps.cz-3A.2* had the most influence on GPS (PVE=52%) and its SS8641 allele decreased GPS, which was opposite to the effect of *OGps.cz-3A.1.* This may be due to environmental difference and $Q \times E$ interaction where *QGps.cz-3A.1* was detected in a warmer location with more precipitation whereas *OGps.cz-3A.2* was detected in a cooler location with less precipitation. The other cluster on 3A was located next to Xbarc45, a marker 8 cM away from Xwmc664 according to the high-density microsatellite consensus map (Somers et al., 2004). Mengistu et al. (2012) found Xwmc664 to be the most significant marker for GPS QTL OKps.neb-3A.1 in a recombinant inbred line population derived from cultivar Cheyenne and its 3A substitution line and that *QKps.neb-3A.1* was in a cluster with nearby QTL. Therefore, it is supposed that the cluster on 3A may represent the same cluster identified by Mengistu et al. (2012). Moreover, Li et al. (2007b) detected two QTLs at the distal end of 3AS. Its estimated position on the microsatellite consensus map was approximately 40 cM based on the information of Xgwm77 (Somers et al., 2004). The cluster identified in this study (OGps.cz-3B.1, OGps.cz-3B.2, and *QGps.cz-3B.3*) was positioned in the same region, suggesting those two clusters may be the same. Another cluster of QTLs with similar influence on GPS was on 5B and the genetic effects of those QTLs were in the same direction. Marza et al. (2006) detected the same region in six environments explaining 18.5% of the phenotypic variation of GYLD. These findings suggested that this cluster improved grain yield by modifying GPS. Additionally, QTLs for GPS or other yield traits have been reported in or close to QGps.cz-2A (Li et al., 2007b), QGps.cz-2B (Marza et al.,

2006), *QGps.cz-4A (Kirigwi et al., 2007), QGps.cz-4A(Huang et al., 2004)*, and *QGps.cz-3D* (Quarrie et al., 2005).

Multiple environment experiments allowed the identification of eight QTLs for GWPS in five environments (Table 2.6). Three closely linked QTLs in which SS8641 alleles increased GWPS were located on 1A and were the strongest QTL associated with GWPS explaining 15.4 to 33.2% of the phenotypic variation. Additional evidence of QTL for GWPS was reported in 3A, 5A and 6B (Zhang et al., 2010). A summary of preceding studies showed that chromosomes 5B and 7B had the fewest number of QTL for yield and yield associated traits (Zhang et al., 2010). Thus, it was not surprising to find no QTLs previously reported in the region of *QGws.cz-5B* and *QGws.cz-7B*.

Under current agricultural production systems, improving spikes m⁻² or grains m⁻² rather than other yield components has been generally agreed to be the key to raising grain yield potential worldwide (Gaju et al., 2009). Therefore, QTL analysis for SPSM has been the target of many studies. Heidari et al. (2011) reported QTLs for SPSM on 1A, 7A, and 2D in a DH population. The QTLs they reported on 1A are comparable to the ones identified at the distal end of 1AS in this study. Marza et al. (2006) found 1B, 4A, 7B and 7D to be associated with SPSM in a wheat population derived from Ning7840 × Clark, where the QTL on 1B was located in the similar region of *Qsm.cz-1B.1* I detected in this study. Similarly, additional SPSM QTLs were located in the region previously described by Huang et al. (2004) on

chromosome 1B, Groos et al. (2003) on chromosome 3B, Bennett et al. (2012b) on chromosomes 3B and 5B, Campbell et al. (2003) on chromosome 3A, Huang et al. (2003) on chromosomes 2A, 2D, and 6D.

Pleiotropic effects of QTLs

Correlated traits are often affected by pleiotropic effects of the same QTL/gene(s) or closely linked QTL/gene(s), which would enable the selection of a complex trait via a closely correlated single trait (Hai et al., 2008). In the present study, a significant positive correlation was observed between GYLD and SPSM in all five environments (Table 2.3) and five loci with genetic effect of same direction were detected for GYLD and SPSM (Table 2.6). Favorable alleles came from both parents. The MDW233 allele increased GYLD and SPSM at *OYld.cz-1A/QSsm.cz.-1A.1*, *OYld.cz-*1B/QSsm.cz.-1B.2, and QYld.cz-6D/QSsm.cz.-6D while the SS8641 allele improved GYLD and SPSM jointly at OYld.cz-2A/OSsm.cz.-2A.1 and OYld.cz-2D/OSsm.cz.-2D. The negative correlation between SPSM and both GWPS and GPS may be due to the pleiotropic effects of loci flanked by Xbar28-Xsnp2005 which increased SPSM but decreased GWPS and GPS or vice versa. These findings supported the existence of a QTL with pleiotropic effect and provided a genetic explanation of observed phenotypic correlation. Although a significant positive correlation was also observed between GYLD and TGW, no pleiotropic QTL was detected. This may indicate that the expression of GYLD was through TGW and conditional mapping was needed to investigate the underlying mechanism (Zhu, 1995).

Q×E and QQ×E interactions

Generally, a QTL with low or no $Q \times E$ interaction can be utilized in a broad range of environments, whereas a QTL with significant $Q \times E$ interaction can only be used in the specific environment in which it is detected (Zhao and Xu, 2012). In this study, the DH population was evaluated in five environments spanning two crop years. Two loci for SPSM, Two for GY and 1 for GPS showed significant additive × environment interaction. The majority of the significant $Q \times E$ effects were found in Queenstown 2013 and Queenstown 2014. Those two environments had relative higher precipitation and average monthly temperature during the growing season indicating that high rainfall and temperature may contribute to $Q \times E$ expression in this study. The intervals Xsnp2427-Xsnp2479 and Xbar28-Xsnp2005 were detected for $Q \times E$ interactions in two environments with opposite effects confirming that the QTL effects were subject to change due to environments and that the environment suitable for the expression of one QTL may not be suitable for another QTL. The SS8641 allele of the locus located in Xbar28-Xsnp2005 was found to be pleiotropic in Oueenstown 2014. It increased GPS but decreased SPSM. However, its $O \times E$ interaction effects were opposite which decreased GPS and increased SPSM, suggesting that the additive effect alone was not enough to characterize the genetic effect of this QTL. It was also apparent that only a small portion of QTL with additive main effect was involved in $Q \times E$ interaction. This suggests that a QTL with no main effects can exercise its effect through interaction with the environment. Therefore, to develop genotypes for target environments or genotypes with broad

adaptation, the $Q \times E$ interaction should be investigated and assessed in plant breeding programs (Basford and Cooper, 1998; El-Soda et al., 2014).

Epistasis has long been recognized to describe a situation where the effect of a particular genotype depends on the genetic background or generally as an interaction between a pair of loci, in which the phenotypic effect of one locus depends on the genotype at the second locus (Bocianowski, 2013; Carlborg and Haley, 2004). Understanding epistasis has been regarded as a necessity to characterize the genetic basis of complex traits (Carlborg and Haley, 2004; Phillips, 2008). Although epistasis was not well investigated in most previous QTL-mapping studies in wheat and its effect may not be as significant (Bennett et al., 2012a; Carter et al., 2011; Heidari et al., 2011; Marza et al., 2006; Mengistu et al., 2012), ignoring epistasis could affect the efficiency and accuracy of MAS as a result of overestimating or underestimating QTL effects (Bocianowski, 2013; Carlborg and Haley, 2004). Also, a simulation study showed that the genetic advance of selection on additive effects became fixed after several cycles of selection when epistasis was present (Wang et al., 2004). In this study, 7 pairs of significant epistatic interactions influencing grain yield and yield components were detected (Table 2.8). However, only two intervals/loci were detected by ICIM-ADD. This suggested many intervals in two locus analysis may escape detection by ICIM-ADD. Kumar et al. (2007) reported similar results and pointed out that this phenomena was more conspicuous in some populations and was perhaps also due to density of map used for QTL analysis. The fact that most epistasis involved only QTL with no main effects indicated that epistasis between non-significant loci may be an important genetic basis of grain yield and yield components in wheat. This has also been found in maize and rice (Li et al., 1997; Ma et al., 2007a; Xing et al., 2014). Besides, it should be noted that the effects of some significant locus (e.g. the one located in *Xbarc28-Xsnp2005*) was completely changed to the opposite direction through interaction with another locus (e.g. the one located in *Xsnp1006-Xsnp823*), implying the need to account for epistasis to avoid an inflated estimate of the net QTL effect. In contrast, the genetic effect of QTL located in *Xsnp3253-Xsnp3349* was enhanced by interacting with the one in *Xsnp3175-Xsnp3401* suggesting that pyramiding QTL/genes could further improve the trait of interest when the direction of epistatic effect among QTL/genes is in the same direction with the additive effects of each QTL/gene involved.

Although both additive and epistatic effects contributed to the phenotypic performance of grain yield and yield components, the contribution from significant epistasis was much smaller compared to that from additive loci for all traits investigated in this study (Figure 2.2), suggesting the essential role of additive main effects in determining yield and yield components in the current DH population and potential targets for MAS. This agreed with recent studies on rice, barley and wheat, where significant epistatic effects for yield and yield components were small in magnitude relative to the additive effects (Wu et al., 2012; Xing et al., 2002; Xu and Jia, 2007; Zhuang et al., 2002). And the low percentage of phenotypic variance explained by epistasis is largely due to a large number of QTLs with small effects (Wu et al., 2012). This might also explain why Q×E and QQ×E interactions were not

examined by researchers in some recent studies in wheat (Carter et al., 2011; Heidari et al., 2011; Kato et al., 2000; Marza et al., 2006).

Conclusion

In the current study the genetic basis of grain yield and yield components in a DH population was investigated by QTL mapping. Significant QTLs for GYLD, GWPS, GPS, SPSM, and TGW were detected almost on every wheat chromosome confirming the general involvement of loci (major QTL clusters and scattered minor QTLs) across the whole genome in the expression of yield and yield components. Although additive main effects, additive × additive epistatic main effects, and their interactions with environments all served as genetic determinants of grain yield and yield components, the additive main effects were the major contributors in this DH population and the magnitude and directions of QTL effects may change due to epistasis and QTL× environment interactions. Additionally, the observed phenotypic correlations between yield and yield components in this study were possibly caused by pleiotropy from QTLs located on 1A, 2A, 2D and 6D. Moreover, a major gene such as *Ppd-D1* was involved in the expression of grain yield per se. Finally, major QTLs identified in this study such as OYld.cz-3B.2 for GYLD and OTgw.cz-7A.5 for TGW could be utilized by breeders for MAS and QTL fine mapping.

Chapter 3: Quantitative trait loci mapping of plant architecture traits in a doubled haploid population of soft red winter wheat

<u>Abstract</u>

Higher wheat grain yields are required to feed an increasing population. An optimized plant architecture may play a crucial role in increasing grain yield. Quantitative trait loci (QTLs) analysis was conducted in a doubled haploid (DH) population to study the genetic basis of plant architecture traits (plant height, PHT; flag leaf length, FLL; flag leaf width, FLW; flag leaf area, FLA; Flag leaf shape (length/width ratio), FLS) across six year-location trials. The DHs showed normal distribution with transgressive segregation, suggesting that plant architecture traits are controlled by polygenes. Seventy four QTLs were detected on all wheat chromosomes. Twenty were for PHT, thirteen were for FLL, sixteen were for FLW, twelve were for FLA, and eleven were for FLS. Major QTLs such as *QPht.cz-2D.2* and QTL clusters on chromosome 2D, 3B, 6A etc. are first reports for plant architecture traits. These QTLs provide useful information for understanding the genetic mechanisms regulating plant architecture in wheat and for marker-assisted selection in designing desirable plant height and flag leaf morphology to increase yield.

Introduction

Plant architecture involves several traits, such as plant height, tillering, branching patterns, leaf size and shape, configuration of leaf relative to the sun and spatial arrangement of leaves (Fageria et al., 2006) and is closely associated with photosynthetic ability and grain yield in wheat (*Triticum aestivum* L.) (Hedden, 2003). Under high soil fertility conditions, the stems of tall plants are generally

unable to support the resultant weight of plump grains and fall over in the field before maturity, a process known as lodging, with consequent large yield losses (Hedden, 2003). This situation was greatly improved after the introduction of dwarfing genes into cereal crops, such as *Rht-B1b* and *Rht-D1b* in wheat and *sd1* in rice which produce semi-dwarf plants with short strong stalks as well as more assimilate partitioned into the grain, leading to large yield increases in wheat and rice known as Green Revolution (Hedden, 2003). However, extremely short plants are disadvantageous because leaves are very closely spaced on a short stem causing increased shading within the canopy, as well as poor ventilation and light transmission in the lower canopy, which affects grain filling and decreases grain yield (Yoshida, 1972; Zhang et al., 2011). Thus, appropriate plant height is a requirement for achieving the desired yield level in wheat breeding programs. The closest leaf from the spike, the flag leaf, is the primary source of assimilates for grain filling and thus grain yield and it also stays green longer than other leaves (Ali et al., 2010). Translocation of carbohydrates from the flag leaf is almost entirely directed towards the grain while that from the lower leaves is only partly directed towards the grain and the detachment of flag leaf considerably decreases grain yield (Ali et al., 2010; Monyo and Whittington, 1973)

Plant height and leaf morphology (flag leaf length, width, and area) are generally considered quantitative traits and influenced by the environment. Understanding the genetic bases of these traits is useful in wheat improvement. To date, more than twenty reduced height genes have been named and some are molecularly

characterized (McIntosh et al., 2013). Height-reducing genes fall into two groups depending on their reaction to endogenous gibberellic acid (GA). Firstly, GAinsensitive genes such as *Rht-B1b* and *Rht-D1b* encode mutant proteins that belong to the DELLA subfamily of GRAS regulatory proteins which repress GA responsive growth by decreasing the sensitivity of vegetative and reproductive tissues to endogenous GA, leading to reduced stem internode length and overall plant height (Tan et al., 2013). Secondly, plants carrying GA-responsive genes, such as *Rht4* and *Rht8*, retain GA responsiveness but show decreased levels of endogenous bioactive GA not due to defective gibberellin biosynthesis or signaling, but possibly to a reduced sensitivity to brassinosteroids (Chen et al., 2015; Gasperini et al., 2012). It should be noted that unfavorable effects such as reduced seedling vigor associated with GA-insensitive genes and delayed anthesis date associated with GA-responsive genes do occur (Chen et al., 2013). Therefore, breeders may need new alternative dwarfing genes to achieve the appropriate height reduction without introducing too much of a negative effect.

In wheat, studies on flag leaf characteristics have focused on their relationship with grain yield and plant adaptation (Blake et al., 2007; Dere and Ylildirim, 2006; Monneveux et al., 2004) and few on QTL analysis. A previous report from Jia et al. (2013a) detected six QTLs for flag leaf length and width among which a major QTL named *QFlw.nau-5A.1* explained 28.7 to 35.6% of the phenotypic variation. *QFlw.nau-5A.1* was inherited like a semidominant gene, designated as *TaFLW1*, and fine mapped in a 0.2 cM interval on chromosome 5A (Xue et al., 2013). The

Wangshuibai *TaFLW1* allele reduced flag leaf width up to 3 mm and was closely linked to the type I Fusarium head blight resistance gene *Fhb5* (Wu et al., 2014; Xue et al., 2013). QTLs controlling leaf morphology have been cloned in rice. A 30-bp deletion in the coding region of rice *Narrow leaf 1(Nal1)* was significantly associated with reduced polar auxin transport capacity which affected the distribution pattern of vascular bundles leading to narrower leaves with fewer longitudinal veins. *NARROW AND ROLLED LEAF 1 (NRL1)*, on rice chromosome 12, encodes the cellulose synthase-like protein D4 (OsCsID4) which plays a crucial role in leaf expansion in rice (Hu et al., 2010). Its three mutants (single base substitutions at three different loci) *nrl1-1, nrl1-2, and nrl1-2* are shorter and show erect, narrow and semi-rolled leaves compared with the *NRL1* carrying plant (Hu et al., 2010).

QTL mapping studies of plant architecture, especially of flag leaf morphology at the whole genome level, have rarely been reported in wheat. To further explore QTLs for plant architecture and provide information for QTL pyramiding, I conducted experiments to map QTLs for plant architecture in a doubled haploid (DH) population of soft red winter wheat. The objective of this study was to identify QTLs with additive effects, epistatic effects, and Q×E interactions for wheat plant height, flag leaf width, length, area, and shape to help design strategies for attaining the desired plant architecture in wheat breeding programs.

<u>Material and Methods</u>

Genetic resources and field experiments

A doubled-haploid population of 124 lines derived from a cross between a soft red winter wheat germplasm line MD01W233-06-1 (MDW233) (Costa et al., 2010) and a soft red winter wheat cultivar SS8641 (Johnson et al., 2007b) was used for this study. MDW233 carries the *Rht-D1b* dwarfing gene the *Ppd-D1b* photoperiod sensitive allele as well as the 1RS/1AL translocation. A genetic linkage map with single nucleotide polymorphism (SNPs), simple sequence repeats (SSRs), and a morphological marker (coleoptile color) was constructed with an average interval length of 2.3 cM (Chapter 2 of this dissertation).

The 124 DH lines, together with the parents MDW233 and SS8641, were planted in the greenhouse and research fields at the University of Maryland. The greenhouse evaluation was carried out in the 2011-2012 and 2012-2013 crop seasons. The population was germinated at room temperature and placed in a growth chamber (4°C, 16 hour light and 8 hour darkness) for eight weeks for vernalization and then transferred to to greenhouse (20°C, 16 hour light and 8 hour darkness) with each line planted in a one-gallon pot. Regular irrigation was used to keep soil moist. Fertilizers were applied directly to each pot in seedling stage. Pots were randomized with three replications in the 2011-2012 season and four replications in the 2012-2013 season. Field tests were conducted in research fields at Clarksville, MD and Queenstown, MD for the 2012-2013 and 2013-2014 crop seasons. The DH lines and two parents evaluated in field plots which were arranged in a randomized complete block design

with two replications. Each field plot consisted of seven rows separated by 15.2 cm. Seed density was 22 seeds per 0.305 m in each row. Growing season rainfall and temperature data were obtained from respective research farms for Clarksville, MD and Queenstown, MD (Figure 3.1). Soil fertility management followed recommended management practices for each location. All trials were sprayed with the metconazole fungicide (Caramba[®], BASF Corporation) at anthesis to reduce potential infection by *Fusarium graminearum*.

Traits and measurements

At maturity, five plants were randomly chosen from each plot of the field study for plant architecture traits evaluation. Plants likely affected by the border effect were avoided. A total of five traits were measured including plant height (PHT, cm), flag leaf length (FLL, cm), flag leaf width (FLW, cm), and flag leaf area (FLA, cm²). FLW was taken at the widest part of the flag leaf. Flag leaf length was measured from the auricle to the apex. Flag leaf area (FLA) was derived (FLA=FLL×FLW×0.79) as previously described (Simpson, 1968; Spagnoletti Zeuli and Qualset, 1990). In the greenhouse study, PHT, FLL, FLW, FLA values were collected from each replication from three individual plants for 2011-2012 and four individual plants for 2012-2013 and averaged for further analyses.

Data analysis

An analysis of variance (ANOVA) for PHT, FLL, FLW, FLA, and FLS was performed separately for each environment and for six environments combined using the PROC GLM procedure of SAS version 9.3 (SAS Institute, Raleigh, NC 2013). The ANOVA model for single environment analysis was Y= replication + genotype + error, where replication and genotype were fixed and error was random. The ANOVA model for combined analysis was Y = environment + replication within environment + genotype + genotype × environment + error, where error was considered random and all others were fixed. Pearson's correlation coefficients were calculated using the PROC CORR procedure of SAS to detect the association among plant architecture traits. Broad-sense heritability (h^2) (defined as $h^2 = \sigma_G^2/(\sigma_G^2 + (\sigma_{GE}^2/e) + (\sigma_E^2/re))$, where σ_G^2 is the variance of genotypic effect, σ_{GE}^2 is the genotype × environment variance, and *e* and *r* are the number of environments and replicates, respectively) for each trait was calculated on a family mean basis using the PROC MIXED procedure of SAS, as described by Holland et al. (2003). The distributions of all evaluated traits were produced using the JMP[®] Pro, Version 11 (SAS Institue, Cary, NC 2014) (Figure 3.2).

QTL analysis

In this study, QTL analysis was performed using IciMapping version 4.0 (Li et al., 2008) for additive effects and QTLNetwork version 2.1 for digenetic QTL epistasis (A×A or Q×Q), additive × environment (A×E or Q×E) and epistasis × environment (QQ×E) interactions (Wang et al., 1999; Yang et al., 2007). For IciMapping version 4.0, inclusive composite interval mapping of additive module (ICIM-ADD) was used and the walking speed for all traits was 1 cM. Reference LOD values were determined by 1, 000 permutations (Doerge, 2002). Type I error to determine the LOD from the permutation test was 0.05. The LOD threshold to declare the presence of a significant QTL was 3.0. The position at which the LOD score curve reached its

maximum was used as the estimate of the QTL location. For QTLNetwork version 2.1, mixed-model based composite interval mapping (MCIM) was used and Q×E, Q×Q, and QQ×E effects were estimated by the Monte Carlo Markov Chain method with a scanning speed of 1 cM step and the experiment-wise type I error for putative QTL detection of 0.05.

<u>Results</u>

Phenotypic data analysis

The performance of the two parents and the DH lines is shown in Figure 3.2. In all six environments, plant architecture traits segregated continuously as typical quantitative traits. Transgressive segregation, progenies with higher or lower phenotype values than the respective parents, was observed for all traits investigated. The ANOVA revealed that the difference between DH lines for all plant architecture traits was highly significant (Table 3.1). Pairwise correlation between plant architecture traits are shown in Table 3.2. Four traits related to flag leaf morphology (FLL, FLW, FLA, and FLS) were significantly intercorrelated across all six environments. Positive correlations were found between FLL and FLW, FLA, and FLS whereas FLW was negatively correlated with FLS. An additional significant negative correlation was identified between PHT and FLW in two of the six environments. The direction of the correlation between FLL and PHT varied among environments.

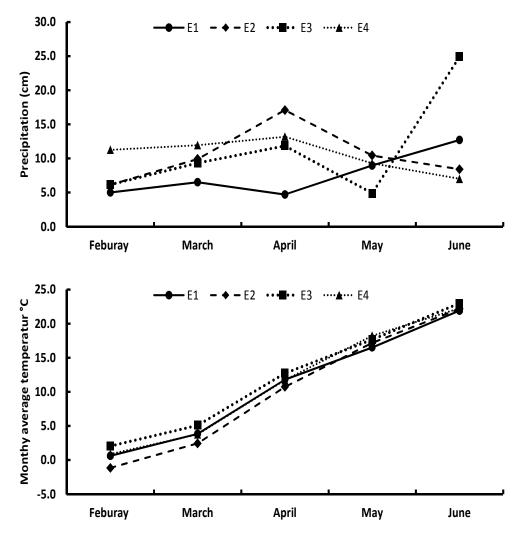


Figure 3.1 Precipitation (unit: cm) and monthly average temperature (unit: °C) during growing season at four field environments: E1, Clarksville, 2013; E2, Clarksville, 2014; E3, Queenstown 2013; E4, Queenstown 2014.

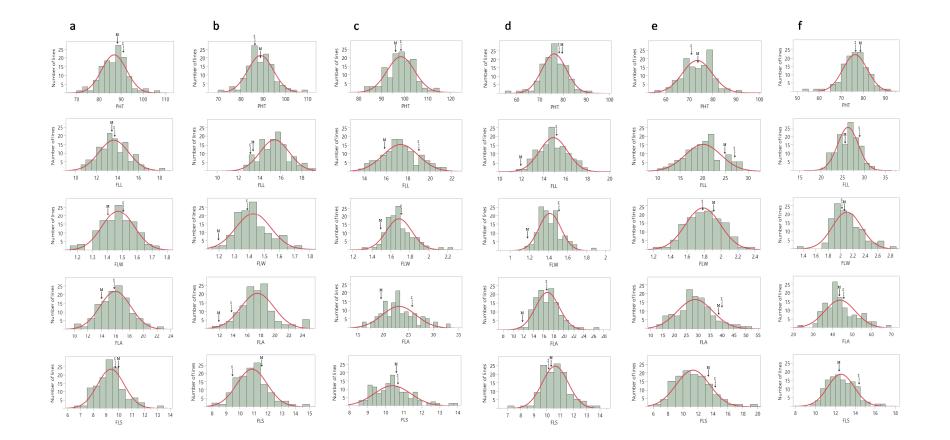


Figure 3.2 Frequency distribution of plant height (PHT, cm), flag leaf length (FLL, cm), flag leaf width (FLW, cm), flag leaf area (FLA, cm²), and flag leaf shape (FLS) of the double haploid lines in a) Clarksville 2013, b) Clarksville 2014, c) Queenstown 2013, d) Queenstown 2014, e) Greenhouse 2012, f) Greenhouse 2013.

Table 3.1 Pooled analyses of variance and heritability estimates for plant height (PHT, cm), flag leaf length (FLL, cm), flag leaf width (FLW, cm), flag leaf area (FLA, cm²), and flag leaf shape (FLS) in four field trials from 2013 to 2014

		Mean Squares				
Source of Variation	df	PH	FLL	FLW	FLA	FLS
Environment	3	20508.86*	578.47*	3.92*	2648.79*	107.89*
Rep(environment)	4	312.84*	23.69*	0.06*	65.26*	3.73*
Genotype	123	212.04*	11.22*	0.08*	38.38*	6.41*
genotype × environment	369	14.70*	1.65*	0.01*	5.42*	0.72*
R^2		0.95	0.88	0.89	0.90	0.86
					0.86	
Heritability $(h^2)^{\dagger}$		0.93(0.01)	0.85(0.02)	0.90(0.2)	(0.02)	0.89(0.02)

* Significant at the 0.001 probability level.

[†] Values in parenthesis are standard errors for h^2

Table 3.2 Pearson correlation coefficients among plant height (PHT, cm), flag leaf length (FLL, cm), flag leaf width (FLW, cm), flag leaf area (FLA, cm²), and flag leaf shape (FLS, cm) in six trials from 2012 to 2014.

Environments	Traits	FLL	FLW	FLA	FLS
Clarksville 2013	PHT	0.24***	-0.07	0.14	0.28***
	FLL		0.26***	0.87***	0.76***
	FLW			0.70***	-0.41***
	FLA				0.35
Clarksville 2014	PHT	0.03	-0.27***	-0.13	0.22*
	FLL		0.29***	0.82***	0.67***
	FLW			0.78***	-0.51***
	FLA				0.12
Queenstown 2013	PHT	0.14	-0.19*	-0.01	0.29***
	FLL		0.38***	0.85***	0.65***
	FLW			0.81***	-0.44***
	FLA				0.16
Queenstown 2014	PHT	0.30***	-0.06	0.16	0.31***
	FLL		0.37***	0.84***	0.60***
	FLW			0.82***	-0.51***
	FLA				0.06
Greenhouse 2012	PHT	-0.19*	-0.13	-0.19*	-0.13
	FLL		0.35***	0.90***	0.81***
	FLW			0.71***	-0.25***
	FLA				0.48***
Greenhouse 2013	PHT	0.21*	-0.06	0.07	0.25***
	FLL		0.50***	0.81***	0.36***
	FLW			0.90***	-0.60***
	FLA				-0.19*

* Significant at the 0.05 probability level. ** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

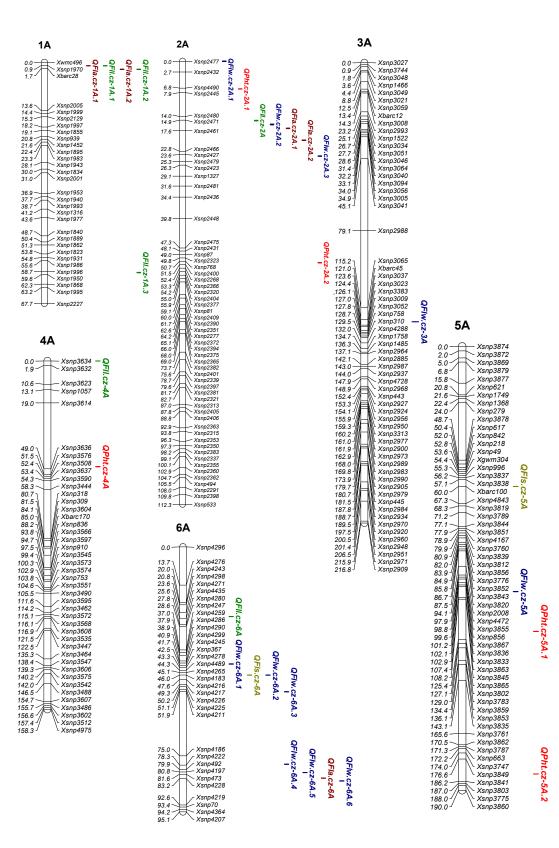
QTLs with additive and additive × environment interaction effects

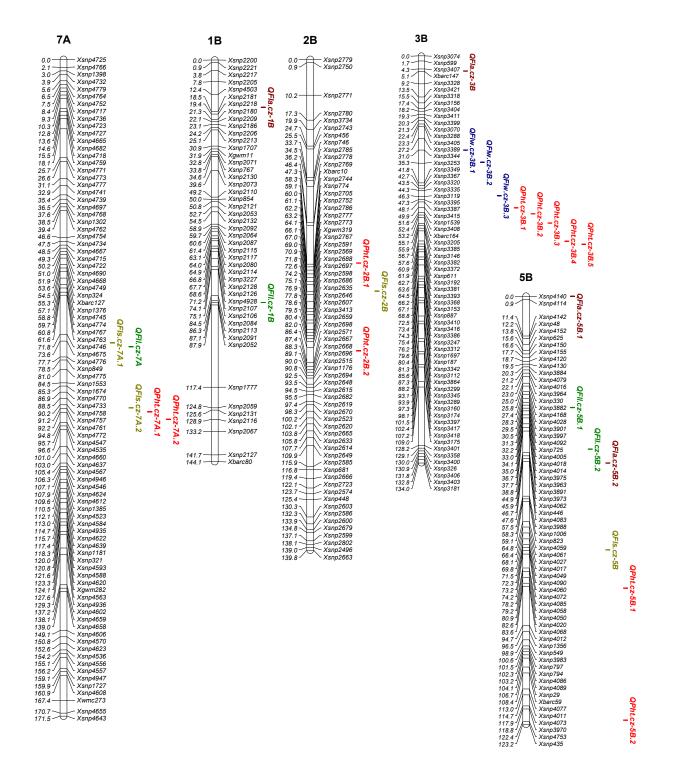
Significant QTLs were detected for all traits evaluated, as summarized in Table 3.3. A total of seventy-four QTLs with additive effects were identified including twenty QTLs for PHT, thirteen for FLL, eighteen for FLW, twelve for FLA, and eleven for FLS. These QTLs were unevenly distributed in the wheat genome. Among them, 35 (47.3%) were in the A genome, 21 (28.4%) were in the B genome, and 18 (24.3%) were in the D genome. The phenotypic variance explained by each QTL ranged from 5.7 to 22% for PHT, 6.4 to 20.7% for FLL, 5.4 to 31.2% for FLW, 6.8 to 24.1% for FLA, and 7.3 to 19.6% for FLS. Both parents contributed favorable alleles (35 from MDW233 and 39 from SS8641). In general, these QTLs had low to moderate genetic effects common for quantitative traits. Additionally, QTL co-localization was found in nine marker intervals suggesting the possible presence of pleiotropy. Mapping QTLs with additive \times environment interaction effects was conducted based on the data from the four field trials only. A total of four intervals were detected with significant Q×E interaction for PHT, FLL, and FLA (Table 3.4). Among them, the loci flanked by XPpdD1-Xsnp2869 and Xsnp1970-Xbarc28 were detected with significant additive effects and other two marker intervals were insignificant for additive effects. The heritability of Q×E interaction ranged from 1% to 2%. Queenstown 2013 had three Q×E interactions and the other three environments each had one.

QTLs with epistatic and epistatic × environment interaction effects

A total of 12 pairs of significant epistatic interactions (p < 0.001) were detected for all five plant architecture traits (Table 3.5). These epistatic interactions involved loci

from within and across chromosomes with heritability values ranging from 0.6% to 4.3%. Among the twenty four epistatic intervals/loci, five were significant for additive effects and the rest were significant only in digenic epistatic interactions. Additionally, an epistatic \times environment interaction was detected between chromosome regions flanked by *Xsnp4061-Xsnp4027* on 5B and *Xsnp4860-Xsnp4831* on 7B at Queenstown 2013 for FLW. However, none of these two intervals were significant for additive main effects.





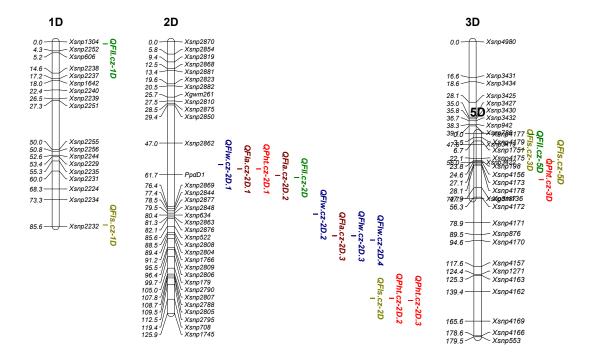


Figure 3.3 Position of quantitative trait loci (QTLs) detected in a doubled haploid mapping population derived from MD01W233-06-1 \times SS8641. Locus marker names are shown on the right side of the chromosomes and values to the left of chromosomes show the genetic distance (cM) for each marker. QTLs are labeled with trait abbreviations and the QTL number for each trait. QTLs for the same trait are in the same color.

Table 3.3 Quantitative trait loci (QTLs) for plant height (PHT, cm), flag leaf length (FLL, cm), flag leaf width (FLW, cm), flag leaf area (FLA, cm²), and flag leaf shape (FLS, cm) in six environments from 2012 to 2014.

QTL	Trait	Environment	Position (cM)	Marker interval	LOD score	PVE (%)	Additive effect
QPht.cz-2A.1	PHT	Clarksville 2013	7	Xsnp4490-Xsnp2445	3.9	5.7	-1.35
QPht.cz-2A.2	PHT	Queenstown 2014	51	Xsnp768-Xsnp2400	3.8	7.6	-1.46
QPht.cz-4A	PHT	Clarksville 2013	48	Xsnp3614-Xsnp3636	4.6	7.0	1.49
QPht.cz-5A.1	PHT	Greenhouse 2012	122	Xsnp3845-Xsnp3865	4.6	10.5	-2.06
QPht.cz-5A.2	PHT	Queenstown 2014	183	Xsnp3849-Xsnp3841	3.3	7.1	1.40
QPht.cz-7A.1	PHT	Clarksville 2013	92	Xsnp4757-Xsnp4761	6.2	9.6	-1.79
QPht.cz-7A.1	PHT	Clarksville 2014	92	Xsnp4757-Xsnp4761	4.6	11.1	-1.95
QPht.cz-7A.2	PHT	Queenstown 2014	94	Xsnp4761-Xsnp4772	5.3	10.8	-1.78
QPht.cz-2B.1	PHT	Clarksville 2013	58	Xbarc10-Xsnp2744	5.2	7.9	1.58
QPht.cz-2B.2	PHT	Queenstown 2013	83	Xsnp2698-Xsnp2571	4.1	9.8	1.86
QPht.cz-3B.1	PHT	Clarksville 2014	50	Xsnp3415-Xsnp1539	6.5	16.0	-2.29
QPht.cz-3B.2	PHT	Clarksville 2013	52	Xsnp1539-Xsnp3408	9.3	15.2	-2.20
QPht.cz-3B.3	PHT	Queenstown 2014	55	Xbarc164-Xsnp3205	4.1	8.0	-1.50
QPht.cz-3B.4	PHT	Greenhouse 2013	61	Xsnp3372-Xsnp611	5.1	13.8	-2.07
QPht.cz-3B.5	PHT	Queenstown 2013	62	Xsnp611-Xsnp3192	4.6	11.1	-1.98
QPht.cz-5B.1	PHT	Greenhouse 2012	84	Xsnp4068-Xsnp4012	9.3	20.1	2.86
QPht.cz-5B.2	PHT	Greenhouse 2012	122	Xsnp3970-Xsnp4753	3.9	7.7	-1.77
QPht.cz-2D.1	PHT	Queenstown 2014	59	Xsnp2862-XPpdD1	7.4	16.6	-2.16
OPht.cz-2D.1	PHT	Clarksville 2013	60	Xsnp2862-XPpdD1	4.9	7.8	-1.58
QPht.cz-2D.2	PHT	Greenhouse 2012	119	Xsnp2795-Xsnp708	9.1	19.5	2.8
QPht.cz-2D.2	PHT	Queenstown 2013	119	Xsnp2795-Xsnp708	8.4	22.0	2.79
OPht.cz-2D.2	PHT	Clarksville 2013	119	Xsnp2795-Xsnp708	6.5	10.2	1.80
QPht.cz-2D.2	PHT	Clarksville 2014	119	Xsnp2795-Xsnp708	3.6	8.6	1.68
OPht.cz-2D.3	PHT	Queenstown 2014	120	Xsnp708-Xsnp1745	7.9	17.1	2.1
QPht.cz-2D.3	PHT	Greenhouse 2013	120	Xsnp708-Xsnp1745	5.8	15.8	2.2
QPht.cz-3D	PHT	Greenhouse 2013	64	Xsnp708-Xsnp1745 Xsnp3422-Xsnp3187	3.3	9.6	1.75
QFlw.cz-2A.1	FLW	Greenhouse 2013	0	Xsnp3422-Xsnp3187 Xsnp2477-Xsnp2432	4.3	9.5	0.00
QFlw.cz-2A.1 QFlw.cz-2A.2	FLW	Greenhouse 2012	16	Xsnp2477-Xsnp2452 Xsnp2471-Xsnp2461	13.3	31.2	0.00
QFlw.cz-2A.2 QFlw.cz-2A.3	FLW		24	Xsnp2477-Xsnp2407 Xsnp2427-Xsnp2479	4.8	11.2	0.1.
	FLW	Queenstown 2013	24 24		4.8	7.1	0.02
QFlw.cz-2A.3		Clarksville 2014	24 24	Xsnp2427-Xsnp2479			
QFlw.cz-2A.3	FLW	Queenstown 2014		Xsnp2427-Xsnp2479	3.6	7.0	0.03
QFlw.cz-2A.3	FLW	Clarksville 2013	24	Xsnp2427-Xsnp2479	3.4	7.3	0.03
QFlw.cz-3A	FLW	Greenhouse 2012	122	Xbarc45-Xsnp3037	5.8	13.4	-0.07
QFlw.cz-5A	FLW	Clarksville 2014	105	Xsnp3833-Xsnp3863	5.2	10.4	0.04
QFlw.cz-6A.1	FLW	Clarksville 2014	42	Xsnp4245-Xsnp367	3.0	5.4	-0.03
QFlw.cz-6A.2	FLW	Queenstown 2014	46	Xsnp4183-Xsnp4216	4.7	9.1	-0.03
QFlw.cz-6A.3	FLW	Clarksville 2013	52	Xsnp4211-Xsnp4186	4.4	9.5	-0.03
QFlw.cz-6A.4	FLW	Queenstown 2013	78	Xsnp4186-Xsnp4222	5.0	11.9	-0.05
QFlw.cz-6A.5	FLW	Greenhouse 2013	81	Xsnp4197-Xsnp473	3.3	6.4	-0.06
QFlw.cz-6A.6	FLW	Clarksville 2014	84	Xsnp4228-Xsnp4219	3.4	6.4	-0.03
QFlw.cz-3B.1	FLW	Clarksville 2014	31	Xsnp3389-Xsnp3344	5.9	11.3	0.04
QFlw.cz-3B.2	FLW	Queenstown 2014	35	Xsnp3344-Xsnp3253	3.6	6.9	0.03
QFlw.cz-3B.3	FLW	Queenstown 2013	46	Xsnp3335-Xsnp3119	3.0	6.9	0.03
QFlw.cz-2D.1	FLW	Clarksville 2013	57	Xsnp2862-XPpdD1	7.0	17.2	-0.05
QFlw.cz-2D.1	FLW	Greenhouse 2013	59	Xsnp2862-XPpdD1	6.5	13.6	-0.09
QFlw.cz-2D.2	FLW	Queenstown 2013	80	Xsnp2848-Xsnp634	3.3	7.5	-0.04
QFlw.cz-2D.3	FLW	Queenstown 2014	90	Xsnp2804-Xsnp1766	9.3	19.9	-0.0
QFlw.cz-2D.3	FLW	Clarksville 2014	91	Xsnp2804-Xsnp1766	4.2	7.7	-0.03
QFlw.cz-2D.4	FLW	Greenhouse 2012	92	Xsnp1766-Xsnp2809	4.5	9.9	-0.00
QFls.cz-2A	FLS	Greenhouse 2013	59	Xsnp2377-Xsnp81	4.5	11.1	-0.44
QFls.cz-5A	FLS	Queenstown 2013	60	Xbarc100-Xsnp4843	4.7	11.7	-0.3
QFls.cz-5A	FLS	Clarksville 2014	61	Xbarc100-Xsnp4843	6.6	19.6	-0.4
QFls.cz-6A	FLS	Greenhouse 2013	46	Xsnp4183-Xsnp4216	4.9	12.3	0.4
QFls.cz-7A.1	FLS	Queenstown 2014	74	Xsnp4675-Xsnp4776	6.3	17.4	-0.4
QFls.cz-7A.2	FLS	Clarksville 2013	91	Xsnp4758-Xsnp4757	7.0	18.2	-0.4
QFls.cz-7A.2	FLS	Queenstown 2013	91	Xsnp4758-Xsnp4757 Xsnp4758-Xsnp4757	5.4	13.7	-0.3
QFls.cz-2B	FLS	Greenhouse 2013	66	Xsnp4730-Xsnp4737 Xsnp2773-Xgwm319	5.0	12.8	-0.3
QFls.cz-2B	FLS	Clarksville 2013	66	Xsnp2773-Xgwm319 Xsnp2773-Xgwm319	3.0	8.3	-0.4
-	FLS		73	Xsnp4090-Xsnp4060			-0.3
QFls.cz-5B		Greenhouse 2012	73 85	Xsnp4090-Xsnp4060 Xsnp2234-Xsnp2232	3.8	11.3	-0.73
QFls.cz-1D	FLS	Queenstown 2013			4.6	11.5	
QFls.cz-2D	FLS	Greenhouse 2013	119	Xsnp2795-Xsnp708	3.0	7.3	0.3
QFls.cz-3D	FLS	Queenstown 2014	50	Xsnp3419-Xsnp3422	3.2	8.5	0.29
QFls.cz-3D	FLS	Greenhouse 2012	56	Xsnp3419-Xsnp3422	3.8	11.1	0.70
QFls.cz-5D	FLS	Clarksville 2014	25	Xsnp4156-Xsnp4173	4.7	12.7	0.3

Table 3.3 Continued

OTL	Trait	Environment	Position	Marker interval	LOD	PVE	Additive
		Environment	(cM)		score	(%)	effect
QFll.cz-1A.1	FLL	Queenstown 2013	1	Xsnp1970-Xbarc28	7.5	18.5	0.69
QFll.cz-1A.1	FLL	Greenhouse 2013	1	Xsnp1970-Xbarc28	4.5	10.0	0.76
QFll.cz-1A.1	FLL	Clarksville 2014	1	Xsnp1970-Xbarc28	3.9	11.5	0.46
QFll.cz-1A.2	FLL	Queenstown 2014	2	Xbarc28-Xsnp2005	6.4	16.0	0.51
QFll.cz-1A.3	FLL	Clarksville 2013	59	Xsnp1996-Xsnp1950	3.1	6.4	0.36
QFll.cz-2A	FLL	Greenhouse 2013	15	Xsnp2471-Xsnp2461	5.2	11.7	0.83
QFll.cz-2A	FLL	Queenstown 2013	16	Xsnp2471-Xsnp2461	3.5	8.2	0.46
QFll.cz-4A	FLL	Greenhouse 2012	0	Xsnp3634-Xsnp3632	3.3	10.2	1.26
QFll.cz-6A	FLL	Greenhouse 2013	25	Xsnp4271-Xsnp4435	4.4	9.7	0.75
QFll.cz-7A	FLL	Clarksville 2013	75	Xsnp4675-Xsnp4776	6.4	14.5	-0.54
QFll.cz-1B	FLL	Queenstown 2014	87	Xsnp2113-Xsnp2091	3.9	9.2	0.39
QFll.cz-5B.1	FLL	Greenhouse 2012	32	Xsnp4092-Xsnp725	5.0	16.3	-1.58
QFll.cz-5B.2	FLL	Clarksville 2013	44	Xsnp3891-Xsnp3973	5.4	12.0	-0.49
QFll.cz-1D	FLL	Greenhouse 2013	1	Xsnp1304-Xsnp2252	3.8	8.5	0.71
QFll.cz-2D	FLL	Queenstown 2013	63	XPpdD1-Xsnp2869	6.2	15.3	-0.63
QFll.cz-2D	FLL	Clarksville 2013	66	XPpdD1-Xsnp2869	7.8	19.6	-0.63
QFll.cz-2D	FLL	Queenstown 2014	70	XPpdD1-Xsnp2869	7.5	20.7	-0.58
QFll.cz-5D	FLL	Clarksville 2014	1	Xsnp4177-Xsnp4179	4.7	14.6	0.53
QFla.cz-1A.1	FLA	Queenstown 2013	1	Xsnp1970-Xbarc28	8.3	16.8	1.36
QFla.cz-1A.2	FLA	Queenstown 2014	2	Xbarc28-Xsnp2005	4.3	9.1	0.70
QFla.cz-2A.1	FLA	Greenhouse 2013	17	Xsnp2471-Xsnp2461	13.1	28.7	4.18
QFla.cz-2A.2	FLA	Queenstown 2013	20	Xsnp2461-Xsnp2466	6.5	13.4	1.23
QFla.cz-6A	FLA	Clarksville 2014	83	Xsnp473-Xsnp4228	3.2	10.1	-0.76
QFla.cz-1B	FLA	Queenstown 2014	17	Xsnp4503-Xsnp2181	4.1	9.4	0.71
QFla.cz-3B	FLA	Greenhouse 2013	5	Xsnp3407-Xbarc147	3.8	6.8	2.03
QFla.cz-5B.1	FLA	Clarksville 2013	0	Xsnp4140-Xsnp4114	3.3	7.9	-0.63
QFla.cz-5B.2	FLA	Greenhouse 2012	48	Xsnp4083-Xsnp3988	3.2	11.4	-2.47
QFla.cz-2D.1	FLA	Queenstown 2013	59	Xsnp2862-XPpdD1	9.5	20.9	-1.53
QFla.cz-2D.2	FLA	Greenhouse 2013	62	XPpdD1-Xsnp2869	5.2	9.7	-2.43
QFla.cz-2D.2	FLA	Queenstown 2014	62	XPpdD1-Xsnp2869	5.0	10.6	-0.77
QFla.cz-2D.2	FLA	Clarksville 2013	63	XPpdD1-Xsnp2869	8.7	24.1	-1.10
QFla.cz-2D.3	FLA	Queenstown 2014	90	Xsnp2804-Xsnp1766	4.6	9.6	-0.72

Table 3.4 QTL × Environment interactions influencing plant height (PHT, cm), flag leaf length (FLL, cm), flag leaf width (FLW, cm), flag leaf area (FLA, cm²), and flag leaf shape (FLS, cm) in four field environments during 2013 and 2014.

Trait	Chr.	Position	Interval	AE1 [†]	$AE2^{\dagger}$	$AE3^{\dagger}$	$AE4^{\dagger}$	h ² (ae) [‡]
PHT	3B	49.9	Xsnp3415-Xsnp1539				0.61*	1.0%
FLL	1A	0.9	Xsnp1970-Xbarc28§			0.16*		1.1%
FLL	2D	66.7	XPpd-D1-Xsnp2869§		0.23*			1.4%
FLA	1A	0	Xwmc496-Xsnp1970 [§]	-0.31*		0.45***		2.0%
FLA	2D	65.7	XPpd-D1-Xsnp2869			-0.33*		1.2%

† AE is the additive × environment interaction effect at each environment. E1: Clarksville 2013; E2: Clarksville 2014; E3: Queenstown 2013; E4: Queenstown 2014.

 $h^2(ac)$ is heritability estimate of the additive × environment interaction effect across four field trails. [§] Interval with significant additive effect. ^{*} Significant at 0.05 probability level.

***Significant at 0.001 probability level.

Table 3.5 Digenetic epistatic QTLs for plant height (PHT, cm), flag leaf length (FLL, cm), flag leaf width (FLW, cm), flag leaf area (FLA, cm²), and flag leaf shape (FLS) in four field trails during 2013 and 2014.

Trait	Interval [†]	Chr. [†]	Position [†]	Interval [‡]	Chr.‡	Position [‡]	AA§	E1¶	E2¶	E3 ¶	E4¶	$h^{2}(aa)^{\#}$	$h^2(aae)^{\dagger\dagger}$
PHT	Xsnp4757-Xsnp4761 ^{‡‡}	7A	91.2	Xsnp3754-Xsnp4981	4D	28	0.72***					1.3%	0.2%
PHT	Xsnp3064-Xsnp3040	3A	31.4	Xsnp849-Xsnp4775	7A	80.5	-1.05***					4.3%	0.1%
PHT	Xsnp3734-Xsnp2743	2B	19.9	Xsnp786-Xsnp3419	3D	39.1	-0.99***					4.7%	0.3%
PHT	Xsnp3389-Xsnp3344 ^{‡‡}	3B	30.2	Xsnp3417-Xsnp3418	3B	102.4	1.04***					4.8%	0.2%
FLL	Xsnp2362-Xsnp494	2A	104.7	Xsnp3444-Xsnp318	4A	73.3	-0.30***					3.4%	0.7%
FLW	Xsnp4763-Xsnp4746	7A	71.6	Xsnp2117-Xsnp2080	1B	63.1	0.02***					2.7%	0.2%
FLW	Xsnp4061-Xsnp4027	5B	66.4	Xsnp4860-Xsnp4831	7B	137.3	0.02***			0.012*		3.5%	0.9%
FLA	Xwmc496-Xsnp1970	1A	0	Xsnp2471-Xsnp2461 ^{‡‡}	2A	15.9	0.27***					0.8%	0.6%
FLA	Xsnp2471-Xsnp2461 ^{‡‡}	2A	15.9	Xsnp4177-Xsnp4179 ^{‡‡}	5D	1	0.29***					1.0%	0.3%
FLA	Xsnp1995-Xsnp2227	1A	63.2	Xsnp2885-Xsnp2987	3A	142.1	-0.41***					2.3%	0.3%
FLS FLS	Xsnp2351-Xsnp2277 Xsnp2401-Xsnp2339	2A 2A	62.6 75.6	Xsnp4444-Xsnp4453 Xsnp4444-Xsnp4453	6B 6B	5.6 5.6	0.14*** -0.29***					0.6% 2.7%	1.4% 1.0%

[†] The flanking markers, chromosome and position of the first interval involved in the epistasis.

[‡] The flanking markers, chromosome and position of the second interval involved in the epistasis.

[§] The additive × additive effect.

¶ The epistasis × environment effect at each environment. E1: Clarksville 2013; E2: Clarksville 2014; E3: Queenstown 2013; E4: Queenstown 2014;

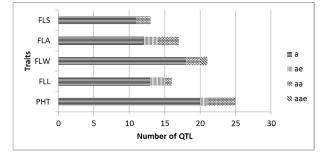
The heritability estimate for additive × additive interaction effects across five environment.

†† The heritability estimate for epistasis × environment interaction effects across four field trials.

‡‡ Interval with significant additive effect.

* Significant at the 0.05 probability level

*** Significant at the 0.001 probability level



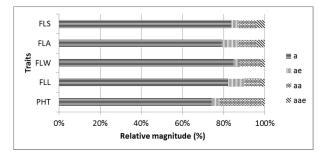


Figure 3.4 Distribution of genetic and non-genetic components for yield and yield related traits: plant height (PHT, cm), Flag leaf length (FLL, cm), Flag leaf width (FLW, cm), Flag leaf area (FLA, cm²), Flag leaf shape (FLS). a) total number of QTLs detected for additive (a), additive \times environment (ae), epistasis (aa), and epistasis \times environment interactions (aae) effects. b) relative magnitude of a, ae, aa, aae effects.

Discussion

Plant architecture is important for grain yield potential in cereal crops. Understanding the genetic control of plant architecture can lay the foundation for further genetic improvement. In this study, a winter wheat DH population was used to study plant architecture traits including PHT, FLL, FLW, FLA, and FLS with the aim of locating the underlying QTLs and to provide targets for marker-assisted selection (MAS) in breeding programs.

QTLs for plant architecture traits

Twenty QTLs for plant height were mapped to chromosomes 2A, 4A, 5A, 7A, 1B, 2B, 5B, 2D, and 3D. A major QTL (*QPht.cz-2D.1*) flanked by *Xsnp2862* and *Ppd-D1* was detected in two environments with high LOD score and PVE (Table 3.3). This region also co-localized with QTLs for FLW and FLA and was closely linked with QTLs for FLL (Figure 3.3). The multiple effects of this region were possibly due to the pleiotropic effects of *Ppd-D1* which is one of the two major genes controlling photoperiod-sensitivity in wheat. Among all alleles of the *Ppd-D1* gene, *Ppd-D1b* is the intact allele and is photoperiod sensitive (Guo et al., 2010) which is also carried by MDW233. *Ppd-D1b* is known to reduce the dates to heading and plant height in many wheat cultivars worldwide (Wilhelm et al., 2013). Similarly, the MDW233 allele of *QPht.cz-2D.1* reduced plant height by an average of 1.87 cm in Queenstown 2014 and Clarksville 2013. Additionally, two other major QTLs (*QPht.cz-2D.2* and *QPht.cz-2D.3*) were detected for PHT, which were about 60 cM downstream of *Ppd-D1b* is for the state of the probability of the the theory of theory of the theory of the theory of theory of theory of theor

environments with an average PVE=10.2%. QPht.cz-2D.3 was detected in two environments with an average PVE of 16.5%. The favorable alleles for these were contributed by SS8641 and both of their additive effects were greater than that of *OPht.cz-2D.1.* In previous studies, Wang et al. (2010) reported a QTL for PHT on 2DS using a winter wheat population and McCartney et al. (2005) detected a QTL on 2DS for PHT using a population generated from the spring wheat cross RL4452 \times 'AC Domain' to study the inheritance of multiple agronomic traits. The location of these two QTLs was very close to the well-known Rht8 gene which is upstream of *Ppd-D1*(Gasperini et al., 2012). Thus, it is possible that QTLs *OPht.cz-2D.2* and *OPht.cz-2D.2*, identified in the present study, are novel loci for PHT. Moreover, *QPht.cz-2D.2* was found to co-localize with *QFll.cz-2D*, a QTL detected for FLS with LOD=4.7 and PVE=12.7 in the 2013 greenhouse study, suggesting the presence of pleiotropy in this loci. Based on these results, *QPht.cz-2D.2* and *QPht.cz-2D.3* are good candidates for fine mapping and gene cloning to get further understanding of their genetic function and develop gene-specific markers for MAS. Additionally, a cluster of five PHT QTLs was detected in a 12.6 cM region on chromosome 3B. Four of them were major QTLs explaining an average of 14% of the phenotypic variation and all their favorable alleles were from MDW233. In this region, QTLs for agronomic traits such as grain yield, thousand grain weight and plant height as well as QTL co-localizations have been reported by several independent studies (Bennett et al., 2012a; Cuthbert et al., 2008; Kumar et al., 2007; Rebetzke et al., 2008). Furthermore, a 2 cM region that contained two QTLs (QPht.cz-7A.1 and QPht.cz-7A.2) on chromosome 7A was significant for PHT. QPht.cz-7A.1 was detected in

Clarksville 2013 and Clarksville 2014 with an average PVE=10.35%. The interaction of QPht.cz-7A.1 with another loci flanked by Xsnp3754-Xsnp4981 on chromosome 4D explained 1.3% of the phenotypic variation of PHT. *OPht.cz-7A.2* was detected in Queenstown 2014 explaining 10.8% of the phenotypic variation. Both favorable alleles in these two loci were from MDW233. McCartney et al. (2005) mapped a QTL, OHt.crc-7A, in the same region for PHT but with a smaller PVE and LOD score. All three QTLs were located around 30 cM downstream of SSR marker barc127 suggesting that QHt.crc-7A may be QPht.cz-7A.1 or QPht.cz-7A.2. Another major QTL, *OPht.cz-5B.1* (LOD=9.3, PVE=20.1%), detected in the present study was comparable to the one identified by Zanke et al. (2014) in a whole genome association mapping of plant height. Previous studies also identified QTLs for plant height or other agronomic traits in the same or nearby region with *OPht.cz-2A.1* (Jia et al., 2013a; Zanke et al., 2014) *QPht.cz-2A.2* (Li et al., 2007b; McCartney et al., 2005), *QPht.cz-2B.1* (Jia et al., 2013a), *QPht.cz-2B.2* (McCartney et al., 2005), *QPht.cz-3D* (Hai et al., 2008), *QPht.cz-4A* (Hai et al., 2008), *QPht.cz-5A.1* (Jia et al., 2013a), *OPht.cz-5A.2* (Huang et al., 2006), *OPht.cz-5B.2* (Zanke et al., 2014).

Although considerable progress has been made in the genetic understanding of grain yield and yield components, reports of QTLs for flag leaf morphology in wheat are still limited. In this study, FLW data was collected from six environments for QTL analysis. *QFlw.cz-2A.2* on chromosome 2A associated with FLW had the largest effect and explained 31.2% of the phenotypic variation in the 2013 greenhouse study. In addition, *QFlw.cz-2A.2* had significant large effects on FLL and FLA with PVE

ranging from 8.2% to 28.7% and also interacted with the loci flanked by Xsnp4177-Xsnp4179 on chromosome 5D to increase FLA. The favorable alleles for FLW, FLL, and FLA at this locus came from SS8641. Given its significant pleiotropic effects, additional markers are needed in order to resolve the QTL position more precisely and to develop reliable diagnostic markers for MAS. In a previous study, Jia et al. (2013a) found this region to be involved in epistatic interactions and contributed to FLL in the Nanda2419×Wangshuibai population. Similarly, in my study, *QFlw.cz*-2A.2 interacted with locus Xsnp4177-Xsnp4179 on chromosome 5D and locus *Xwmc496-Xsnp1970* on chromosome 1A to contribute to the expression of FLA. In the nearby region of *QFlw.cz-2A.2*, a consistent QTL *QFlw.cz-2A.3* was detected. *OFlw.cz-2A.3* was significant for FLW in all four field environments with LOD score ranging from 3.4 to 4.8 and was related to the QTLs associated with plant height (Kulwal et al., 2003) and yield components (Zhang et al., 2010). On chromosome 2D, there were two major QTLs: OFlw.cz-2D.1 and OFlw.cz-2D.3. OFlw.cz-2D.1 colocalized with OPht.cz-2D.1. OFlw.cz-2D.3 was co-located with OFla.cz-2D.3 for FLA with favorable alleles from MDW233. In the same region with *QFlw.cz-2D.3/ QFla.cz-2D*, a QTL with additive effects for FLL, FLW, and heat susceptibility index (HIS) was reported by Mason et al. (2013) where its Halberd allele was favorable for a longer or wider flag leaf and also improved heat tolerance. It was noticeable that FLW QTLs on chromosome 6A had same direction additive effects as well as the ones on 3B but the direction associated with QTLs on 6A was opposite to that of QTLs on 3B suggesting an antagonistic relationship. Other major QTLs associated with FLW, such as *QFlw.cz-3A* and *QFlw.cz-5A*, were related to grain yield, grains

m⁻², spikes m⁻², and grains per spike as reported by Dilbirligi et al. (2006) and Kato et al. (2000).

Thirteen QTLs were detected for FLL. The MDW233 alleles increased FLL at four loci located on chromosomes 7A, 5B, and 2D accounting for 14.4-20.7% of the phenotypic variation whereas SS8641 increased FLL at the other nine loci on 1A, 2A, 4A, 6A, 1B, 1D, and 5D, accounting for 6.4-18.5% of the phenotypic variation. Among them, two QTLs (QFll.cz-1A.1 and QFll.cz-1A.2) on chromosome 1A overlapped at *Xbarc28* which also flanked *OFla.cz-1A.1* and *OFla.cz-1A.2* for FLA. At these four loci, favorable alleles were from SS8641 and explained 9.1-18.5% of the phenotypic variation. In previous studies, *Xbarc28* was also linked to QTLs for spike length (Marza et al., 2006). Additionally, the same region was also associated with QTLs and meta-QTLs for yield components (Zhang et al., 2010). These results suggested the existence of important genes/QTLs and that high resolution mapping would be necessary to determine if the effects were due to pleiotropy or closely linked QTLs. Two major QTLs on chromosome 4A and 5B contributed more than 1 cm to FLL in the 2012 greenhouse study. The SS8641 allele increased FLL at OFIL.cz-4A but decreased FLL at QFIL.cz-5B.1. Both of these two QTLs were located in the same region associated with agronomic traits such as spike length, spike compactness, and plant height (Sourdille et al., 2003). Moreover, major QTL OFIL.cz-5D was significant for both additive and epistatic interaction effects. This same region was also reported to contain QTLs for grain quality traits related to dough physical properties (Huang et al., 2006) and epistatic QTLs for yield related traits

such as grains spike⁻¹ and 100-grain weight (Jia et al., 2013a). Furthermore, a PHT QTL on chromosome 7A (McCartney et al., 2005) was located in the same region as *QFII.cz-7A* identified in this study. This region, flanked by *Ppd-D1-Xsnp2869*, was associated with both FLL and FLA explaining an average of 16.6% of the phenotypic variation across four environments. This is possibly due to the pleiotropic effects of *Ppd-D1* which accelerates wheat development in long days and affects the number of leaf and spikelet primordia number (Borràs-Gelonch et al., 2012; Foulkes et al., 2004).

QTLs for the derived traits FLS and FLA were also identified. Of the eleven QTLs detected for FLS, nine (81.8%) explained more than 10% of the phenotypic variation and QTLs on 5A, 7A, 2B, and 3D were detected in more than one environment. In addition, the twelve QTLs identified for FLA explained, on average, 13.5% of the phenotypic variation. To my knowledge, these are some of the first QTLs reported for these leaf morphology traits in wheat.

Genetic complexity of plant architecture

Compared with studies involving only additive QTLs (Bian et al., 2014; Xue et al., 2008a), I also examined epistatic effects and their interactions with environment revealing additional information on the genetic composition of plant architecture traits. In the six environments included in this study, seventy four additive QTLs and twelve pairs of epistatic QTLs were identified. Among them four additive QTLs and one pair of epistatic QTLs interacted with the environment. The results showed that both additive and epistatic effects were essential genetic bases of wheat plant

architecture and their effects were subject to environment modifications. The relative magnitude of these effects is shown in Figure 3.4. This indicated that, among all genetic effects, additive effects were the main contributors (>70%) to plant architecture variation in this DH population. It is interesting to note that only four significant additive QTLs were involved in epistatic interactions suggesting that epistasis can contribute to quantitative traits expression through the interactions of non-significant loci. Similarly, Zhang et al. (2008) found that 25% of additive-effect QTLs were involved in the epistatic interactions in wheat plant height. Additionally, I found that the locus flanked by Xsnp3389-Xsnp3344 (significant additive effect for FLW) on 2B and the locus flanked by Xsnp4177-Xsnp4179 (significant additive effect for FLL) on 5D, contributed to PHT and FLA respectively, when they were involved in epistatic interactions. This suggests that QTLs may express pleiotropic effects through their interactions with other loci. Furthermore, the additive effect of *OPht.cz-7A.1* was reduced after taking into account its epistatic interaction with the locus flanked by Xsnp3754-Xsnp4981 and that the additive effect of OFla.cz-2A.1 was enhanced by interacting with *QFll.cz-5D*. These antagonistic and synergistic epistatic interactions not only added complexity to the genetic control of plant architecture traits but also provides important information for designing schemes to pyramid beneficial alleles in breeding programs.

Conclusion

This study is one of the few dedicated to QTL mapping of plant architecture traits in hexaploid wheat. I identified several new QTLs and QTL clusters that were shown to affect the expression of PHT, FLL, FLW, FLA, and FLS such as *QPht.cz-2D.2* for

PHT, *QFll.cz-1A.1* for FLL, and the QTL clusters on chromosome 6A and 3B for FLW. Those QTLs could be used for marker assisted selection in breeding programs to modify plant architecture traits.

Chapter 4: Quantitative trait loci mapping of spike characteristics in a doubled haploid population of soft red winter wheat

<u>Abstract</u>

Understanding the genetic basis of spike characteristics in wheat is important for breeding wheat cultivars with higher yield potential. In this study, a doubled haploid population of 124 lines was used to evaluate six spike traits 1) spike length (SL), 2) fertile spikelet number per spike (FSN), 3) sterile spikelet number per spike (SSN), 4) total spikelet number per spike (TSN), 5) spike compactness (SC), and 6) grains per spikelet (GSP). Quantitative trait loci (QTL) mapping was conducted based on the data collected from five year-location trials. A total of 109 QTLs were detected for all traits. In addition, 13 QTL-by-environment and 20 epistatic interactions were also identified. Major QTLs QSl.cz-1A/ QFsn.cz-1A for SL and FSN explained up to 30.9% of the phenotypic variation, QGsp.cz-2B.1 for GSP explained up to 15.6% of the phenotypic variation, and QSc.cz-5A.3 for SC explained up to 80.2% of the phenotypic variation. When combining the digenic interaction effect, the average contribution of *QFsn.cz-1A* to FSN in each environment was enhanced by 19%. QTLs for correlated traits in the same genomic region formed QTL clusters on chromosomes 1A, 5A, 2B, 3B, 5B, 1D, and 5D. The findings of this study will aid in the improvement of wheat spike characteristics and hence the grain yield potential in breeding programs.

Introduction

Wheat (Triticum aestivum L.) is a major food crop across the globe. Improving its yield potential has irrefutable importance in meeting the food demand from increasing population worldwide. The grain yield of wheat is largely determined by yield components out of which the three most important are spikes per unit area, grains per spike, and grain weight (Dilbirligi et al., 2006; Mengistu et al., 2012). Previous studies have shown that grain yield variation is mostly associated with grain number changes where grain number, expressed as grains m^{-2} , is the product of spikes m^{-2} and grains per spike and that there appears to be less opportunity for genetic yield improvement by selecting heavier grains (Fischer, 2011; Frederick and Bauer, 1999). Increases in grains per spike or/and spikes m⁻² have contributed to wheat yield improvement in the past decades (Ma et al., 2007b). Spike characteristics including spike length (SL), total spikelet number per spike (TSN), fertile spikelet number per spike (FSN), sterile spikelet number per spike (SSN), spike compactness (SC), and grains per spikelet (GSP) determine the number of grains per spike, and thus, to a certain extent, determine the yield potential.

Spike characteristics are quantitative traits under quantitative trait loci (QTL) control and subject to environmental influence (Cui et al., 2012; Ma et al., 2007b). Genetic dissection of spike characteristics could facilitate improving grain yield potential of wheat. Several domestication genes, such as Q, compactum (C), and sphaerococcum (S1) are related to wheat spike morphology and have been identified on chromosomes 5A, 2D, and 3D respectively (Faris et al., 2003; Faris and Gill, 2002; Johnson et al.,

2007a; Rao, 1977). The Q gene confers a free-threshing spike and pleiotropically influences many other domestication related traits, including plant height, glume keeledness, rachis toughness, spike type and spike emergence time, resulting in tougher stems and higher yields (Faris et al., 2003; Simons et al., 2006; Sormacheva et al., 2014). The C gene is located on the long arm of chromosome 2D near the centromere and affects spike compactness, grain size, grain shape, and grain number per spike (Johnson et al., 2007a). The SI gene confers rigid short culms, straight flag leaves, dense spikes, hemispherical glumes, and small spherical grains (Rao, 1977). In addition to these loci, previous studies have identified genomic regions associated with spike-related traits on all twenty one wheat chromosomes (Borner et al., 2002; Cui et al., 2012; Deng et al., 2011; Kumar et al., 2007; Ma et al., 2007b; Marza et al., 2006; Wang et al., 2011). For example, Cui et al. (2012) detected 190 QTLs across all wheat chromosomes for seven spike-related traits in two recombinant inbred line populations. Eighteen of the detected QTLs were major QTLs and were significant across multiple environments. Ma et al. (2007b) investigated the additive, dominant and epistatic effects of QTLs for SL, FSN, SSN, TSN, and SC in a recombinant inbred line population and also from an immortalized F₂ population derived from the same parents and found 18 genomic regions on chromosomes 1A, 1B, 2D, 3B, 4A, 5A, 5B, and 7A to be associated with spike characteristics. Additionally, Kumar et al. (2007) identified QTLs for SL on chromosomes 1A, 1B, 1D, 2B, 2D, 4A, 5A, and 5D and QTLs for TSN on 2D, 4A, 4D, 5A, and 6A. These results demonstrated that multiple loci with unequal effects can affect spike traits and that epistasis and dominance effects are also indisputable components of genetic architecture of spike

characteristics. Furthermore, mapping agronomically important QTLs as Mendelian factors in wheat was also reported by Uauy et al. (2006) after rice (Ashikari et al., 2005) and tomato (Frary et al., 2000). Similarly, Deng et al. (2011) investigated wheat spike traits in a F₂ population, derived from the cross between an elite cultivar Laizhou953 and an introgression line 05210 (in Laizhou953 background). This population showed a clear 3:1 segregation ratio for spike number per plant, spike length, and grain number per spike. The underlying QTL was mapped to chromosome 4B and explained 30.1 to 67.6% of the phenotypic variation in two environments. Fine mapping and molecular characterization of this region have not been reported yet.

In this study, I used a doubled haploid population derived from two soft red winter wheat cultivars that showed a wide range of phenotypic variation for spike characteristics. A previously constructed linkage map that spanned 1978 cM was used to study the genetic basis of six spike traits (Chapter 2 of this dissertation). The objectives of this study were to identify QTLs affecting spike characteristics as well as their closely linked markers for use by breeding programs and future fine mapping.

Materials and Methods

Genetic resources and phenotypic traits evaluation

A doubled-haploid (DH) population derived from a cross between a soft red winter wheat germplasm line MD01W233-06-1 (MDW233) (Costa et al., 2010) and a soft red winter wheat cultivar SS8641 (Johnson et al., 2007b) was used. MDW233 carries the *Rht-D1b* dwarfing gene the *Ppd-D1b* photoperiod sensitive allele as well as the

1RS/1AL translocation. A genetic linkage map with single nucleotide polymorphism (SNPs), simple sequence repeats (SSRs), and a morphological marker (coleoptile color) was previously constructed with an average interval length of 2.3 cM.

The DH population, comprised of 124 lines, and its two parents were evaluated at five year-location environments in Maryland and North Carolina: Clarksville, MD 2013 (E1), Clarksville, MD 2014 (E2), Queenstown, MD 2013 (E3), Queenstown, MD 2014 (E4), and Kinston, NC 2014 (E5). The population was grown in field plots arranged in a randomized complete block design with two replications. Each field plot consisted of seven rows separated by 15.2 cm. Seed density was 22 seeds per 0.305 m in each row. Soil fertility management followed recommended management practices for each location. All trials were sprayed with the metconazole fungicide (Caramba[®], BASF Corporation) at anthesis to reduce potential infection by *Fusarium graminearum* and other diseases.

Ten plants in the middle rows from each plot were randomly selected for spike traits evaluation. Traits examined included spike length (SL) in centimeters, measured from the base of the rachis to the top of the uppermost spikelet, fertile spikelet number per spike (FSN), and sterile spikelet number per spike (SSN). Total spikelet number per spike (TSN) was equal to FSN plus SSN. Spike compactness (SC) was derived by dividing TSN by SL and grains per spikelet (GSP) was derived by dividing grain number per spike by FSN.

Phenotypic data analysis

Phenotypic data analysis was performed using SAS version 9.3 (SAS Institute, Raleigh, NC 2013) to compare differences among DH lines and environments. Phenotypic value for SL, FSN, SSN, TSN, SC, and GSP for 10 plants from each DH line in each replication was averaged before analyses. Simple summary statistics for six spike traits were calculated by the PROC MEANS procedure of SAS. Analysis of variance (ANOVA) for SL, FSN, SSN, TSN, SC, and GSP was performed separately for each environment and for five environments combined by the PROC GLM procedure. The linear model for ANOVA for single environment analysis was $Y_{ii}=\mu$ $+ g_i + r_i + \varepsilon_{ij}$, where μ is the overall mean, Y_{ij} is the phenotypic value of the ith DH line in jth replication, g_i is the fixed effect of the ith DH line, r_i is the fixed effects of jth replication, and ε_{ij} is the random effects of error associated with Y_{ij} and for combined analysis $Y_{ijk} = \mu + g_i + r_{jk} + e_k + \varepsilon_{ijk}$, where μ is the overall mean, Y_{ijk} is the phenotypic value of the ith DH line in jth replication of kth environment, g_i is the fixed effect of the ith DH line, r_{ik} is the fixed effects of jth replication of kth environment, e_k is the fixed effect of the k^{th} environment, and ε_{ijk} is the random effect of error associated with Y_{ijk}. Pearson's correlation coefficients were calculated by the PROC CORR procedure to detect the association among spike traits. Broad-sense heritability (h^2) (defined as $h^2 = \sigma_G^2 / (\sigma_G^2 + (\sigma_{GE}^2/e) + (\sigma_E^2/re))$, where σ_G^2 is the variance of genotypic effect, σ_{GE}^2 is the genotype \times environment variance, and e and r are the number of environments and replicates, respectively) for each trait was calculated on a family mean basis by the PROC MIXED procedure, as described by Holland et al. (2003).

QTL detection

Mapping QTLs for spike characteristics was performed using two methods. First, inclusive composite interval mapping (ICIM) was conducted to detect QTLs with additive effects by the ICIM-ADD module of IciMapping version 4.0 (Li et al., 2008). The walking speed for all traits was 1 cM. Reference LOD values were determined by 1, 000 permutations (Doerge, 2002). Type I error to determine the LOD from the permutation test was 0.05 and the LOD threshold to declare the presence of a significant QTL was 3.0. Secondly, QTL epistasis (Q×Q), QTL× environment (Q×E) and epistasis × environment (QQ×E) interaction effects were detected by QTLNetwork version 2.1 using a mixed-model based composite interval mapping (MCIM) (Wang et al., 1999; Yang et al., 2007). Q×E, Q×Q, and QQ×E effects were estimated by the Monte Carlo Markov Chain method with a scanning speed of 1 cM step with the experiment-wise type I error for putative QTL detection of 0.05. In both methods, the position at which the LOD score curve reached its maximum was used as the estimate of the QTL location.

<u>Results</u>

Phenotypic analysis

Five different field trials were conducted at three locations over two years to evaluate spike characteristics of the DH population as well as the parental genotypes MDW233 and SS8641. Mean values of traits at each trial are shown in Table 4.1. SS8641 had longer spikes, also more fertile and total spikelets per spike as well as more grains per spikelet; MDW233 had more sterile spikelets per spike. The compactness was similar between the parents. In all trials, the DH population showed

significant variation and transgressive segregation was obvious with data distributed beyond the parental values, suggesting polygenic inheritance of the investigated traits (Table 4.1). ANOVA results showed that significant differences existed between DH lines and between environments at p < 0.001 level in the performance of six spike traits (Table 4.2). Estimates of heritability (on a family mean basis) of the traits varied from trait to trait, ranging from 88% to 95%. The TSN had the highest heritability of 95% whereas GSP had the lowest (Table 4.2). Correlation coefficients among the spike traits in different trials are presented in Table 4.3. SL showed a significant positive correlation with FSN and TSN but a negative correlation with SC across all five environments. There was a positive correlation between TSN and FSN. A positive correlation was also found between TSN and SC. SC was positively correlated with SSN, FSN and TSN in almost all of the environments. GSP was negatively correlated with SSN and had no significant relationships with both SL and FSN except in E3. Significant negative correlations were also observed between GSP and TSN in E1 and E2 so was GSP and SC in E1, E2, and E3. The strongest correlation was observed between TSN and FSN.

Table 4.1 Phenotypic values for spike characteristics: spike length (SL, cm), sterile spikelet number per spike (SSN), fertile spikelet number per spike (FSN), total spikelet number per spike (TSN), spikelet compactness (SC), and grain number per spikelet (GSP) in the MD01W233-06-1 × SS8641 doubled haploid population evaluated in five field trials from 2013 to 2014: Clarksville 2013 (E1), Clarksville 2014 (E2), Queenstown 2013 (E3), Queenstown 2014 (E4), Kinston 2014 (E5).

		Parents		DH lines				
Traits	Environments	MDW233	SS8641	Mean	Std. Dev.	Minimum	Maximum	CV§
SL	E1	6.6	7.3	7.0	0.5	5.7	8.4	7.5%
	E2	6.9	7.7	7.3	0.5	6.3	8.5	6.9%
	E3	7.0	8.0	7.2	0.5	6.0	8.6	7.3%
	E4	6.1	6.9	6.8	0.5	5.6	8.3	7.5%
	E5	7.1	8.4	7.5	0.5	6.2	9.0	7.1%
FSN	E1	13.0	15.7	14.3	1.1	11.8	17.3	7.6%
	E2	14.4	16.5	15.2	0.9	13.0	17.6	6.0%
	E3	14.6	16.3	14.9	1.0	12.5	17.4	6.8%
	E4	12.5	13.8	14.0	0.9	11.5	16.2	6.3%
	E5	14.8	17.0	16.1	1.2	13.7	20.2	7.4%
SSN	E1	2.1	1.8	1.8	0.5	0.8	3.1	25.4%
	E2	1.9	1.8	2.2	0.4	1.3	3.6	20.3%
	E3	1.6	1.1	1.7	0.5	0.3	3.5	31.8%
	E4	1.6	1.5	1.2	0.4	0.3	2.5	34.1%
	E5	2.5	1.8	2.4	0.6	1.2	4.1	23.0%
TSN	E1	15.1	17.5	16.2	1.1	14.1	19.2	6.6%
	E2	16.2	18.3	17.4	1.0	15.2	20.2	5.6%
	E3	16.1	17.4	16.6	1.1	14.3	19.4	6.5%
	E4	14.0	15.3	15.2	0.9	13.0	17.7	6.0%
	E5	17.2	18.8	18.5	1.3	16.1	22.3	6.9%
SC	E1	2.3	2.4	2.3	0.2	2.0	2.9	6.5%
	E2	2.4	2.4	2.4	0.1	2.0	2.8	5.5%
	E3	2.3	2.2	2.3	0.1	1.9	2.7	6.4%
	E4	2.3	2.2	2.3	0.1	2.0	2.6	5.3%
	E5	2.4	2.2	2.5	0.2	2.1	3.0	6.7%
GSP	E1	2.7	2.9	2.8	0.2	2.1	3.3	8.5%
	E2	2.3	2.4	2.2	0.2	1.8	2.6	8.1%
	E3	3.0	3.1	2.8	0.3	2.2	3.4	9.2%
	E4 E5	2.8 2.4	2.8 2.7	2.8 2.6	0.2 0.2	2.3 2.3	3.3 3.2	7.1% 7.2%

§ coefficient of variation

Table 4.2 Pooled analysis of variance and heritability estimates for spike characteristics: spike length (SL, cm), sterile spikelet number per spike (SSN), fertile spikelet number per spike (FSN), total spikelet number per spike (TSN), spikelet compactness (SC), and grain number per spikelet (GSP) in the MD01W233-06-1 × SS8641 doubled haploid population evaluated in five field trials from 2013 to 2014.

		Mean	square				
Source of Variation	df	SL	SSN	FSN	TSN	SC	SSP
Environment	4	20.82***	55.20***	161.70***	388.27***	1.71***	17.08***
Rep (environment)	5	0.89***	2.74***	4.41***	4.68***	0.05***	3.62***
Genotype	123	2.25***	1.65***	7.94***	8.92***	0.17***	0.31***
Genotype × environment	492	0.11***	0.18***	0.64***	0.63***	0.01***	0.04***
\mathbb{R}^2		0.91	0.87	0.89	0.95	0.91	0.91
Heritability (h^2)		0.95 (0.01)	0.89 (0.02)	0.92 (0.01)	0.92 (0.01)	0.94 (0.01)	0.88 (0.02)

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

Table 4.3 Pearson correlation coefficients among spike characteristics: spike length (SL, cm), sterile spikelet number per spike (SSN), fertile spikelet number per spike (FSN), total spikelet number per spike (TSN), spikelet compactness (SC) in the MD01W233-06-1 \times SS8641 the doubled haploid population evaluated in five field trials from 2013 to 2014.

Environments		SSN	FSN	TSN	SC	GSP
Clarksville 2013	SL	-0.26**	0.68***	0.58***	-0.55***	0.14
	SSN		-0.26**	0.17	0.47***	-0.39***
	FSN			0.91***	0.15	-0.05
	TSN				0.36***	-0.22*
	SC					-0.38***
Clarksville 2014	SL	0.00	0.66***	0.61***	-0.60***	0.07
	SSN		-0.09	0.37***	0.36***	-0.62***
	FSN			0.89***	0.10	0.05
	TSN				0.25**	-0.23*
	SC					-0.31***
Queenstown 2013	SL	-0.18*	0.71***	0.58***	-0.56***	0.25**
	SSN		-0.14	0.37***	0.56***	-0.62***
	FSN			0.87***	0.07	0.23**
	TSN				0.35***	-0.09
	SC					-0.36***
Queenstown 2014	SL	0.03	0.71***	0.71***	-0.60***	0.06
	SSN		-0.19*	0.27**	0.27**	-0.39***
	FSN			0.90***	0.01	0.15
	TSN				0.13	-0.03
	SC					-0.12
Kinston 2014	SL	-0.05	0.62***	0.55***	-0.50***	0.13
	SSN		-0.06	0.38***	0.45***	-0.40***
	FSN			0.90***	0.27**	0.16
	TSN				0.44***	-0.03
	SC					-0.16

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

QTL detection

Up to 109 putative additive QTLs for the six spike traits were detected by ICIM (Table 4.4) and their map positions are shown in Figure 4.1. The number of QTLs detected for each trait ranged from 16 to 22, specifically, 20 for FSN, 12 for SC, 20 for SL, 19 for SSN, 16 for GSP, and 22 for TSN. These QTLs were located on 15 chromosomes and formed QTL clusters. In addition, 21 regions were detected to be associated with more than one trait.

Spike length

Twenty chromosome regions were identified to govern SL in the present study. Chromosome 1A and 1D each had one QTL. Chromosome 3A and 6A each had two QTLs. Three QTLs were detected on each of the chromosomes 3B, 2D, and 5D, and five QTLs were detected on 5A. Major QTLs (PVE>10%) for SL were identified on chromosomes 1A, 5A, 6A, 3B, and 5D. SS8641 alleles were associated with longer spikes at seventeen (85%) loci whereas MDW233 alleles were associated with longer spike at the other three loci on chromosome 2D. QTL *QSl.cz-1A* was detected in four environments (E1, E2, E3, and E5) and mapped to the interval *Xsnp1970- Xbarc28* on chromosome 1A (Figure 4.1), explaining 9.2-23.6% of the phenotypic variation of SL. This QTL was also significantly associated with FSN and TSN, respectively. In all cases, the favorable alleles were contributed by SS8641 and the additive effects of *QSl.cz-1A* were the largest among all QTLs for SL, FSN, and TSN suggesting an essential region for spike characteristics. Major SL QTL *QSl.cz-3B.1* localized in the

same interval with FSN QTL *QFsn.cz-3B.1*. QTLs formed clusters on chromosomes 5D, 3B, and 5A.

Spike compactness

Twelve QTLs, distributed on six chromosomes, were significantly associated with SC. The major QTL *QSc.cz-5A.3* was detected in E2, E3, and E5 and had mostly large additive effects explaining up to 80.2% of the phenotypic variation. *QSc.cz-5A.1* also explained a large portion of the observed variation (26.7%) in E1. Additionally, *QSc.cz-5A.3* clustered with *QSc.cz-5A.1* and *QSc.cz-5A.2*. Clustering of consistent major QTLs was also identified on chromosome 2B and 5D. MDW233 contributed positive alleles at clusters on 5A and 5D whereas SS8641 increased SC at loci on chromosome 3A, 2B, 5B, and 6D.

Grains per spikelet

Sixteen QTLs were detected for GSP. They were distributed on chromosomes 1A, 5A, 6A, 7A, 2B, 3B, 5B, 6B, 1D, and 2D. QTL *QGsp.cz-2B.1* was detected in E1, E3, E4, and E5 accounting for 6.0-15.6% of the phenotypic variation and mapped to a position close to the major QTL *QGsp.cz-2B.2* (LOD=7.4, PVE=13.7%). Four major QTLs mapped to similar positions and overlapped along the short arm of chromosome 5B explaining 11.6 to 14.5% of the phenotypic variation. Another two major QTLs *QGsp.cz-1A.2* and *QGsp.cz-2D* explained 14.2 to 15.5% of the phenotypic variation, respectively. SS8641 contributed favorable alleles for QTLs on chromosomes 1A, 3B, 6B, and 2D.

Fertile spikelet number per spike

Twenty QTLs significantly influenced FSN and mapped to nine chromosomes. QTLs on chromosomes 2D and 2A favored high FSN through MDW233 alleles and the rest were associated with high FSN through SS8641 alleles except for QTL *QFsn.cz-5A.1*.The QTL on chromosome 1A, mapped to the interval *Xsnp1970-Xbarc28*, consistently showed a large effect on FSN. Another consistent QTL *QFsn.cz-2D.2* was mapped to chromosome 2D with a LOD score of 3.3 to 5.3. For *QFsn.cz-2D.2*, the MDW233 allele increased FSN. The remaining QTLs were detected in only one environment. There were six major QTLs for FSN and the phenotypic variation explained by each individual QTL ranged from 10.4 to 30.9%.

Sterile spikelet number per spike

Nineteen QTLs were associated with SSN. For the QTLs located on chromosome 2A, 2B, 5B, and 3D, the SS8641 allele increased SSN, whereas for the QTLs on 1A, 3A, 2D, and 6D, the MDW233 alleles increased SSN. The phenotypic variation explained by these individual QTLs ranged from 3.7 to 30%. QTL *QSsn.cz-2B.2* was identified in E1, E2, E3, and E4 as a major QTL, sharing this interval with *QTsn.cz-2B.3* and *QSc.cz-2B.3*. QTL *QSsn.cz-1A* was coincident with *QGsp.cz-1A.2*. At locus *Ppd-D1*, *QSsn.cz-2D.1* and *QSsn.cz-2D.2* overlapped, each explaining 30% and 7.5% of the phenotypic variation, respectively.

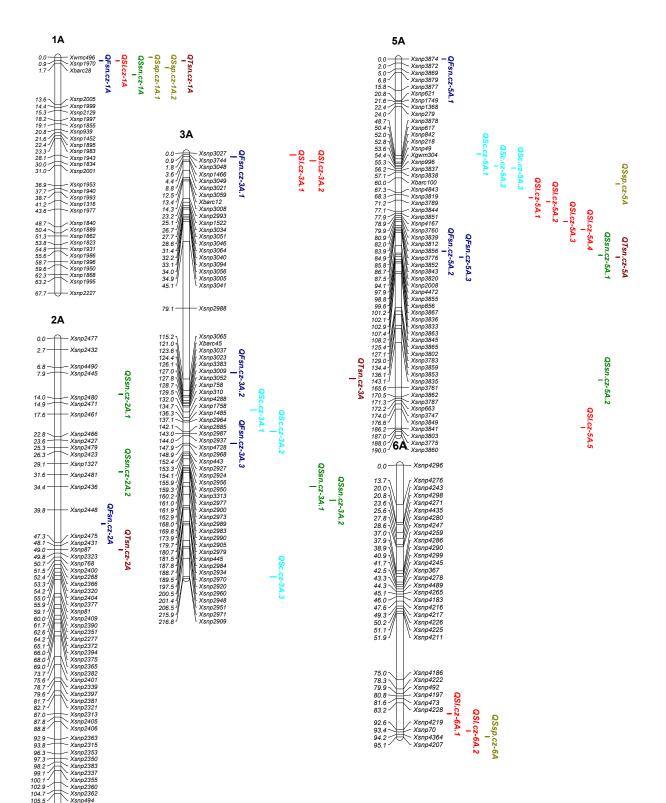
Total spikelet number per spike

Twenty-two chromosome regions were associated with TSN. However, seventeen of them were only detected once. Consistent QTLs included *QTsn.cz-1A*, *QTsn.cz-2D.2*, *QTsn.cz-2D.3*, *QTsn.cz-2D.4* and *QTsn.ca-5D.1* explaining 8.4 to 20.9% of the

phenotypic variation. For QTLs detected on chromosome 2A, 6B, and 2D, MDW233 alleles decreased TSN. SS8641alleles increased TSN at the remaining loci. QTL clusters were found on chromosomes 2B, 2D, and 5D and the genetic effects of QTLs in each cluster were in the same direction.

$QTL \times$ environment, epistasis, and epistasis \times environment interactions

In this study, I used a mixed-model based composite interval mapping method to estimate the QTL× environment (Q×E), epistasis (Q×Q), and epistasis× environment (QQ×E) interactions. Thirteen Q×E interactions were detected for SSN, FSN, and TSN, out of which eleven involved intervals associated with significant additive effects. The other two were non-significant QTLs (LOD<3) for additive effects. E4, E5, and E3 each had six, five, and two Q×E interactions, respectively. No Q×E interaction was detected in E1 and E2. The contribution of Q×E interactions ranged from 0.6-2.2%. Twenty pairs of Q×Q interactions were also identified (Table 4.6). Twelve intervals involved in Q×E interactions were significant for additive effects. The heritability estimates of Q×Q and QQ×E interactions ranged from 0.3 to 4.9% and 0.9 to 1.4%.

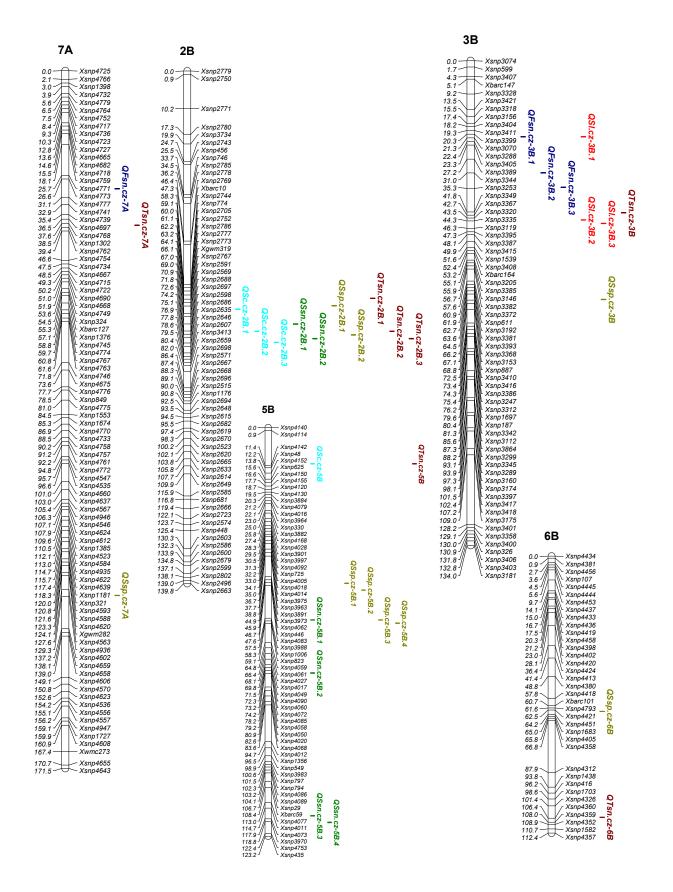


108.0 Xsnp2291 - Xsnp2398 109.8 U

112.3

- Xsnp533

109



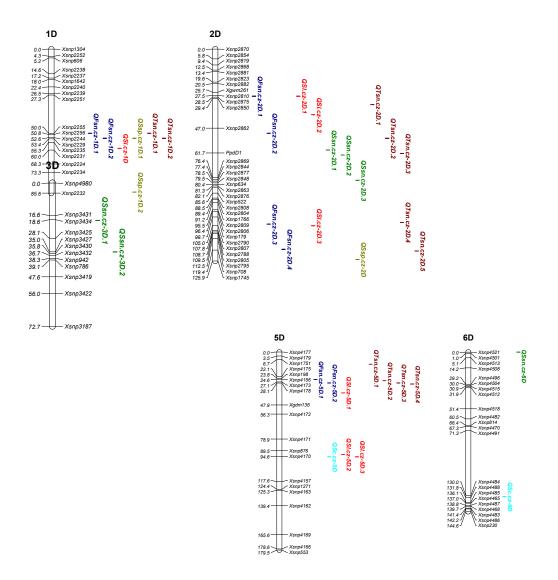


Figure 4.1 Position of quantitative trait loci (QTLs) detected in a doubled haploid mapping population derived from MD01W233-06-1 × SS8641. Locus marker names are shown on the right side of the chromosomes and values to the left of chromosomes show the genetic distance (cM) for each marker. QTLs are labeled with trait abbreviations and the QTL number for each trait. QTLs for the same trait are in the same color.

Table 4.4 Quantitative trait loci (QTLs) for spike characteristics: spike length (SL, cm), sterile spikelet number per spike (SSN), fertile spikelet number per spike (FSN), total spikelet number per spike (TSN), spikelet compactness (SC), and grain number per spikelet (GSP) in the MD01W233-06-1 \times SS8641 doubled haploid population evaluated in five field trials from 2013 to 2014.

QTL	Trait	Environment	Position (cM)	Marker interval	LOD score	PVE (%)	Additive effect
QSl.cz-1A	SL	Clarksville 2013	1	Xsnp1970-Xbarc28	11.6	23.6	0.25
QSl.cz-1A	SL	Clarksville 2014	1	Xsnp1970-Xbarc28	5.7	11.1	0.17
QSl.cz-1A	SL	Kinston 2014	1	Xsnp1970-Xbarc28	6.1	9.2	0.16
QSl.cz-1A	SL	Queenstown 2013	1	Xsnp1970-Xbarc28	9.3	22.4	0.25
QSl.cz-3A.1	SL	Clarksville 2013	1	Xsnp3744-Xsnp3048	3.7	6.5	0.13
QSl.cz-3A.2	SL	Kinston 2014	4	Xsnp1466-Xsnp3049	5.0	7.3	0.15
QSl.cz-5A.1	SL	Kinston 2014	70	Xsnp3819-Xsnp3789	8.2	13.0	0.20
QSI.cz-5A.1	SL	Queenstown 2013	71	Xsnp3819-Xsnp3789	5.0	11.0	0.18
QSl.cz-5A.2	SL	Clarksville 2014	72	Xsnp3789-Xsnp3844	6.2	12.5	0.18
QSl.cz-5A.3	SL	Queenstown 2014	82	Xsnp3812-Xsnp3856	4.0	9.7	0.16
QSl.cz-5A.4	SL	Clarksville 2013	86	Xsnp3852-Xsnp3843	7.0	13.1	0.19
OSl.cz-5A.5	SL	Queenstown 2014	186	Xsnp3849-Xsnp3841	2.8	6.7	0.13
QSI.cz-6A.1	SL	Queenstown 2013	87	Xsnp4228-Xsnp4219	3.4	7.8	0.15
QSI.cz-6A.2	SL	Clarksville 2013	93	Xsnp4219-Xsnp70	6.0	11.0	0.17
QSI.cz-3B.1	SL	Queenstown 2014	21	Xsnp3399-Xsnp3070	5.5	13.9	0.19
QSI.cz-3B.2	SL	Clarksville 2013	44	Xsnp3320-Xsnp3335	5.3	9.5	0.16
QSI.cz-3B.2	SL	Kinston 2014	44	Xsnp3320-Xsnp3335	6.6	9.9	0.10
QSI.cz-3B.3	SL	Clarksville 2014	45	Xsnp3335-Xsnp3119	3.0	6.0	0.12
QSI.cz-3B.3	SL	Queenstown 2013	45	Xsnp3335-Xsnp3119	5.4	12.1	0.12
QSI.cz-1D	SL	Kinston 2014	59	Xsnp2235-Xsnp2231	4.4	6.5	0.13
QSI.cz-2D.1	SL	Kinston 2014	28	Xsnp2235-Xsnp2231 Xsnp2810-Xsnp2875	2.7	0.3 3.7	-0.11
QSI.cz-2D.1 QSI.cz-2D.2	SL	Clarksville 2013	28 39	Xsnp2850-Xsnp2862	2.9	5.5	-0.11
QSI.cz-2D.2 QSI.cz-2D.3	SL SL	Clarksville 2013	105	Xsnp179-Xsnp2790	3.0	5.6	-0.12
-		Clarksville 2014	105 37	1 1			
QSI.cz-5D.1	SL			Xsnp4178-Xgdm136	6.1	13.5	0.18
QSI.cz-5D.2	SL	Queenstown 2014	93 95	Xsnp876-Xsnp4170	4.7	12.0	0.17
QSI.cz-5D.3	SL	Kinston 2014		Xsnp4170-Xsnp4157	4.0	5.8	0.13
QFsn.cz-1A	FSN	Clarksville 2013	1	Xsnp1970-Xbarc28	14.2	30.9	0.60
QFsn.cz-1A	FSN	Clarksville 2014	1	Xsnp1970-Xbarc28	9.4	16.7	0.37
QFsn.cz-1A	FSN	Kinston 2014	1	Xsnp1970-Xbarc28	20.6	30.0	0.65
QFsn.cz-1A	FSN	Queenstown 2013	1	Xsnp1970-Xbarc28	11.2	23.9	0.49
QFsn.cz-2A	FSN	Clarksville 2014	43	Xsnp2448-Xsnp2475	4.2	7.2	-0.25
QFsn.cz-3A.1	FSN	Kinston 2014	2	Xsnp3048-Xsnp1466	3.9	4.1	0.24
QFsn.cz-3A.2	FSN	Clarksville 2013	112	Xsnp2988-Xsnp3065	6.1	12.4	0.39
QFsn.cz-3A.3	FSN	Kinston 2014	148	Xsnp4728-Xsnp2968	5.0	5.3	0.27
QFsn.cz-5A.1	FSN	Kinston 2014	0	Xsnp3874-Xsnp3872	4.3	4.5	-0.25
QFsn.cz-5A.2	FSN	Clarksville 2014	97	Xsnp2008-Xsnp4472	2.8	4.5	0.20
QFsn.cz-5A.3	FSN	Queenstown 2014	100	Xsnp856-Xsnp3867	3.2	9.3	0.27
QFsn.cz-7A	FSN	Clarksville 2014	29	Xsnp4773-Xsnp4777	4.1	6.9	0.24
QFsn.cz-3B.1	FSN	Queenstown 2014	21	Xsnp3399-Xsnp3070	2.8	8.1	0.25
QFsn.cz-3B.2	FSN	Kinston 2014	31	Xsnp3389-Xsnp3344	4.1	4.3	0.25
QFsn.cz-3B.3	FSN	Queenstown 2013	35	Xsnp3344-Xsnp3253	4.7	8.9	0.30
QFsn.cz-1D.1	FSN	Clarksville 2013	50	Xsnp2251-Xsnp2255	3.6	6.3	0.27
QFsn.cz-1D.2	FSN	Kinston 2014	53	Xsnp2244-Xsnp2229	10.4	12.4	0.41
QFsn.cz-2D.1	FSN	Kinston 2014	28	Xsnp2810-Xsnp2875	3.2	3.3	-0.22
QFsn.cz-2D.2	FSN	Clarksville 2013	50	Xsnp2862-XPpdD1	3.3	6.3	-0.28
QFsn.cz-2D.2	FSN	Queenstown 2013	56	Xsnp2862-XPpdD1	5.3	10.4	-0.33
QFsn.cz-2D.3	FSN	Clarksville 2014	104	Xsnp179-Xsnp2790	6.7	11.6	-0.31
QFsn.cz-2D.4	FSN	Kinston 2014	119	Xsnp2795-Xsnp708	3.6	3.7	-0.23
QFsn.cz-5D.1	FSN	Queenstown 2014	25	Xsnp4156-Xsnp4173	2.7	7.7	0.25
QFsn.cz-5D.2	FSN	Clarksville 2014	28	Xsnp4173-Xsnp4178	7.4	12.6	0.33

Table 4.4 Continued

QTL	Trait	Environment	Position (cM)	Marker interval	LOD score	PVE (%)	Additiv effe
QSsn.cz-1A	SSN	Clarksville 2013	5	Xbarc28-Xsnp2005	2.6	7.0	-0.1
QSsn.cz-2A.1	SSN	Kinston 2014	13	Xsnp2445-Xsnp2480	3.8	5.4	0.1
QSsn.cz-2A.2	SSN	Queenstown 2014	31	Xsnp1327-Xsnp2481	4.8	7.7	0.1
QSsn.cz-3A.1	SSN	Queenstown 2014	170	Xsnp2983-Xsnp2990	8.1	13.8	-0.1
QSsn.cz-3A.2	SSN	Clarksville 2013	177	Xsnp2990-Xsnp2905	3.9	9.8	-0.1
QSsn.cz-5A.1	SSN	Kinston 2014	99	Xsnp3855-Xsnp856	5.8	8.4	-0.1
QSsn.cz-5A.2	SSN	Kinston 2014	162	Xsnp3835-Xsnp3761	3.2	4.8	0.1
QSsn.cz-2B.1	SSN	Kinston 2014	69	Xsnp2767-Xsnp2591	8.5	13.0	0.2
QSsn.cz-2B.2	SSN	Clarksville 2014	73	Xsnp2697-Xsnp2598	5.3	14.4	0.1
QSsn.cz-2B.2	SSN	Clarksville 2013	74	Xsnp2697-Xsnp2598	5.2	12.9	0.
QSsn.cz-2B.2	SSN	Queenstown 2013	74	Xsnp2697-Xsnp2598	6.3	18.3	0.2
QSsn.cz-2B.2	SSN	Queenstown 2014	74	Xsnp2697-Xsnp2598	3.2	5.1	0.0
QSsn.cz-5B.1	SSN	Clarksville 2014	58	Xsnp3988-Xsnp1006	2.9	7.5	0.1
QSsn.cz-5B.2	SSN	Queenstown 2014	74	Xsnp4060-Xsnp4072	4.5	7.5	0.1
QSsn.cz-5B.3	SSN	Kinston 2014	117	Xsnp4011-Xsnp4073	4.8	6.8	0.1
QSsn.cz-5B.4	SSN	Queenstown 2014	119	Xsnp3970-Xsnp4753	6.0	10.0	0.1
QSsn.cz-2D.1	SSN	Kinston 2014	60	Xsnp2862-XPpdD1	16.3	30.0	-0.3
QSsn.cz-2D.2	SSN	Queenstown 2014	63	XPpdD1-Xsnp2869	4.5	7.5	-0.1
QSsn.cz-2D.3	SSN	Clarksville 2013	78	Xsnp2844-Xsnp2877	5.6	14.4	-0.
QSsn.cz-2D.3	SSN	Queenstown 2013	78	Xsnp2844-Xsnp2877	3.6	10.2	-0.
QSsn.cz-3D.1	SSN	Kinston 2014	19	Xsnp3434-Xsnp3425	2.7	3.7	0.
QSsn.cz-3D.2	SSN	Clarksville 2014	35	Xsnp3427-Xsnp3430	2.7	6.8	0.
QSsn.cz-6D	SSN	Queenstown 2014	0	Xsnp4521-Xsnp4501	3.1	4.8	-0.
QTsn.cz-1A	TSN	Clarksville 2013	1	Xsnp1970-Xbarc28	9.5	19.7	0.4
QTsn.cz-1A	TSN	Clarksville 2014	1	Xsnp1970-Xbarc28	5.9	8.4	0.2
QTsn.cz-1A	TSN	Kinston 2014	1	Xsnp1970-Xbarc28	13.2	20.0	0.5
QTsn.cz-1A	TSN	Queenstown 2013	1	Xsnp1970-Xbarc28	9.3	14.1	0.4
QTsn.cz-2A	TSN	Clarksville 2014	49	Xsnp87-Xsnp2323	6.2	8.8	-0.2
QTsn.cz-3A	TSN	Clarksville 2013	115	Xsnp2988-Xsnp3065	5.4	10.3	0.
QTsn.cz-5A	TSN	Queenstown 2014	100	Xsnp856-Xsnp3867	2.8	7.4	0.2
QTsn.cz-7A	TSN	Clarksville 2014	38	Xsnp4768-Xsnp1302	5.2	7.4	0.2
QTsn.cz-2B.1	TSN	Clarksville 2014	62	Xsnp2752-Xsnp2786	2.8	3.8	0.
QTsn.cz-2B.2	TSN	Queenstown 2013	71	Xsnp2569-Xsnp2688	3.5	4.8	0.2
QTsn.cz-2B.3	TSN	Clarksville 2013	73	Xsnp2697-Xsnp2598	3.5	6.4	0.2
QTsn.cz-3B	TSN	Queenstown 2013	42	Xsnp3349-Xsnp3367	3.5	4.6	0.2
QTsn.cz-5B	TSN	Kinston 2014	11	Xsnp4114-Xsnp4142	2.9	3.6	0.
QTsn.cz-6B	TSN	Queenstown 2013	106	Xsnp4326-Xsnp4360	3.2	4.4	-0.2
QTsn.cz-1D.1	TSN	Clarksville 2013	50	Xsnp2251-Xsnp2255	3.1	5.7	0.2
QTsn.cz-1D.2	TSN	Kinston 2014	53	Xsnp2244-Xsnp2229	5.7	7.4	0.1
QTsn.cz-2D.1	TSN	Kinston 2014	33	Xsnp2850-Xsnp2862	3.8	5.2	-0.
QTsn.cz-2D.2	TSN	Clarksville 2013	53	Xsnp2862-XPpdD1	5.4	11.2	-0.
QTsn.cz-2D.2	TSN	Queenstown 2013	59	Xsnp2862-XPpdD1	9.4	14.7	-0
QTsn.cz-2D.3	TSN	Clarksville 2014	62	XPpdD1-Xsnp2869	4.2	5.9	-0.
QTsn.cz-2D.3	TSN	Kinston 2014	63	XPpdD1-Xsnp2869	8.1	11.5	-0
QTsn.cz-2D.3	TSN	Queenstown 2014	68	XPpdD1-Xsnp2869	6.5	20.9	-0.4
QTsn.cz-2D.4	TSN	Clarksville 2014	103	Xsnp179-Xsnp2790	4.9	7.4	-0.2
QTsn.cz-2D.4	TSN	Queenstown 2013	105	Xsnp179-Xsnp2790	3.8	5.1	-0.
QTsn.cz-2D.5	TSN	Kinston 2014	120	Xsnp708-Xsnp1745	4.8	6.5	-0
QTsn.cz-5D.1	TSN	Clarksville 2013	120	Xsnp1751-Xsnp4175	2.6	5.0	-0.
QTsn.cz-5D.1	TSN	Kinston 2014	11	Xsnp1751-Xsnp4175 Xsnp1751-Xsnp4175	3.6	5.0	0.1
QTsn.cz-5D.2	TSN	Queenstown 2014	26	Xsnp1/51-Xsnp41/5 Xsnp4156-Xsnp4173	4.6	12.6	0.
QTsn.cz-5D.2	TSN	Clarksville 2014	28	Xsnp4173-Xsnp4178	11.6	18.4	0.4
~ · ··································	1014	Charksville 2017	20	Xsnp4175-Xsnp4178 Xsnp4178-Xgdm136	5.0	7.1	0.

QTL	Trait	Environment	Position (cM)	Marker interval	LOD score	PVE (%)	Additive effect
QSc.cz-3A.1	SC	Clarksville 2013	131	Xsnp310-Xsnp4288	4.1	7.7	0.04
QSc.cz-3A.2	SC	Clarksville 2014	142	Xsnp2964-Xsnp2885	5.0	8.8	0.04
QSc.cz-3A.2	SC	Queenstown 2013	142	Xsnp2964-Xsnp2885	3.6	7.4	0.04
QSc.cz-3A.3	SC	Kinston 2014	216	Xsnp2971-Xsnp2909	3.7	6.5	0.04
QSc.cz-5A.1	SC	Kinston 2014	48	Xsnp279-Xsnp3878	12.7	26.7	0.09
QSc.cz-5A.2	SC	Clarksville 2013	54	Xsnp49-Xgwm304	6.3	12.7	-0.05
QSc.cz-5A.2	SC	Queenstown 2014	54	Xsnp49-Xgwm304	3.8	9.3	-0.04
QSc.cz-5A.3	SC	Clarksville 2014	55	Xgwm304-Xsnp996	10.9	21.9	-0.06
QSc.cz-5A.3	SC	Kinston 2014	55	Xgwm304-Xsnp996	27.7	80.2	-0.15
QSc.cz-5A.3	SC	Queenstown 2013	55	Xgwm304-Xsnp996	6.0	13.0	-0.05
QSc.cz-2B.1	SC	Queenstown 2014	65	Xsnp2773-Xgwm319	5.8	15.4	0.05
QSc.cz-2B.1	SC	Clarksville 2013	66	Xsnp2773-Xgwm319	8.7	18.3	0.06
QSc.cz-2B.1	SC	Queenstown 2013	66	Xsnp2773-Xgwm319	9.3	21.6	0.07
QSc.cz-2B.2	SC	Kinston 2014	71	Xsnp2569-Xsnp2688	9.4	18.2	0.07
QSc.cz-2B.3	SC	Clarksville 2014	74	Xsnp2697-Xsnp2598	7.2	13.2	0.05
QSc.cz-5B	SC	Clarksville 2014	11	Xsnp4114-Xsnp4142	3.1	5.3	0.03
QSc.cz-5D	SC	Clarksville 2014	95	Xsnp4170-Xsnp4157	3.3	5.7	-0.03
QSc.cz-5D	SC	Kinston 2014	95	Xsnp4170-Xsnp4157	7.4	13.9	-0.06
QSc.cz-5D	SC	Queenstown 2014	95	Xsnp4170-Xsnp4157	6.6	16.8	-0.05
QSc.cz-5D	SC	Clarksville 2013	99	Xsnp4170-Xsnp4157	2.8	5.6	-0.04
QSc.cz-5D	SC	Queenstown 2013	100	Xsnp4170-Xsnp4157	3.5	8.1	-0.04
QSc.cz-6D	SC	Clarksville 2013	131	Xsnp4484-Xsnp4488	3.1	5.8	0.04
QGsp.cz-1A.1	GSP	Clarksville 2013	0	Xwmc496-Xsnp1970	3.6	6.7	0.06
QGsp.cz-1A.2	GSP	Queenstown 2013	3	Xbarc28-Xsnp2005	5.6	14.2	0.10
QGsp.cz-1A.2	GSP	Clarksville 2014	5	Xbarc28-Xsnp2005	6.1	13.3	0.06
QGsp.cz-5A	GSP	Queenstown 2014	63	Xbarc100-Xsnp4843	3.8	9.7	-0.06
QGsp.cz-6A	GSP	Kinston 2014	95	Xsnp4364-Xsnp4207	2.9	7.4	-0.05
QGsp.cz-7A	GSP	Queenstown 2014	129	Xsnp4563-Xsnp4936	3.8	9.0	-0.06
QGsp.cz-2B.1	GSP	Clarksville 2013	64	Xsnp2777-Xsnp2773	3.2	6.0	-0.06
QGsp.cz-2B.1	GSP	Kinston 2014	64	Xsnp2777-Xsnp2773	5.8	15.6	-0.08
QGsp.cz-2B.1	GSP	Queenstown 2013	64	Xsnp2777-Xsnp2773	5.4	12.9	-0.09
QGsp.cz-2B.1	GSP	Queenstown 2014	64	Xsnp2777-Xsnp2773	4.2	9.9	-0.06
QGsp.cz-2B.2	GSP	Clarksville 2014	72	Xsnp2688-Xsnp2697	7.4	13.7	-0.07
QGsp.cz-3B	GSP	Clarksville 2014	66	Xsnp3393-Xsnp3368	4.3	7.7	0.05
QGsp.cz-5B.1	GSP	Queenstown 2014	47	Xsnp446-Xsnp4083	4.8	11.6	-0.07
QGsp.cz-5B.2	GSP	Clarksville 2013	49	Xsnp4083-Xsnp3988	5.7	12.0	-0.08
QGsp.cz-5B.3	GSP	Clarksville 2014	58	Xsnp3988-Xsnp1006	7.7	14.5	-0.07
QGsp.cz-5B.4	GSP	Kinston 2014	59	Xsnp1006-Xsnp823	4.7	12.5	-0.07
QGsp.cz-5B.4	GSP	Queenstown 2013	59	Xsnp1006-Xsnp823	3.4	7.9	-0.07
QGsp.cz-6B	GSP	Clarksville 2013	63	Xsnp4421-Xsnp4451	2.7	5.3	0.05
QGsp.cz-1D.1	GSP	Queenstown 2013	53	Xsnp2244-Xsnp2229	2.7	6.0	-0.06
QGsp.cz-1D.2	GSP	Clarksville 2014	85	Xsnp2234-Xsnp2232	4.1	7.1	-0.05
QGsp.cz-2D	GSP	Clarksville 2013	125	Xsnp708-Xsnp1745	7.5	15.5	0.09

Trait	QTL	Interval	Position	$AE1^{\dagger}$	$AE2^{\dagger}$	$AE3^{\dagger}$	$AE4^{\dagger}$	$AE5^{\dagger}$	$h^2(ae)^{\ddagger}$
SSN	5A	Xsnp3820-Xsnp2008	92.5				0.05*		0.9%
SSN	2B	Xsnp2591-Xsnp2569	69				-0.05*		0.7%
SSN	2D	Ppd-D1-Xsnp2869§	67.7					-0.12***	2.0%
FSN	1A	Xsnp1970-Xbarc28 [§]	0.9				-0.22***	0.14**	2.2%
FSN	2A	Xsnp2448-Xsnp2475 [§]	44.8			0.10*			0.6%
FSN	1D	Xsnp2244-Xsnp2229§	52.6				-0.10*	0.11*	0.9%
TSN	1A	Xsnp1970-Xbarc28 [§]	0.9				-0.15***	0.13*	1.2%
TSN	2D	Xsnp2850-Xsnp2862§	34.4			-0.12*	0.19**	-0.16**	1.8%

Table 4.5 QTL × Environment interactions influencing spike characteristics: spike length (SL, cm), sterile spikelet number per spike (SSN), fertile spikelet number per spike (FSN), total spikelet number per spike (TSN), spikelet compactness (SC) and grain number per spikelet (GSP) in the MD01W233-06-1 × SS8641 doubled haploid population evaluated in five field trials from 2013 to 2014.

 \dagger AE is the additive \times environment interaction effect at each environment. E1: Clarksville 2013; E2: Clarksville 2014; E3: Queenstown 2013; E4: Queenstown 2014.

 $\ddagger h^2(ae)$ is heritability estimate of the additive \times environment interaction effect across four field trails.

[§] Interval with significant additive effect. * Significant at the 0.05 probability level **Significant at the 0.01 probability level ** *Significant at the 0.001 probability level

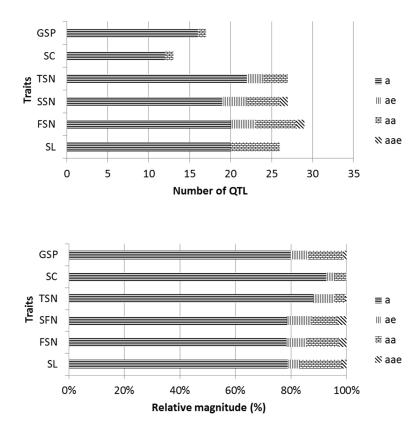


Figure 4.2 Distribution of genetic and non-genetic components for yield and yield related traits: spike length (SL, cm), sterile spikelet number per spike (SSN), fertile spikelet number per spike (FSN), total spikelet number per spike (TSN), spikelet compactness (SC), and grain number per spikelet (GSP). a) total number of QTLs detected for additive (*a*), additive × environment (*ae*), epistasis (*aa*), and epistasis × environment interactions (*aae*) effects. b) relative magnitude of *a*, *ae*, *aa*, *aae* effects.

Table 4.6 Digenic epistatic QTLs for spike characteristics: spike length (SL, cm), sterile spikelet number per spike (SSN), fertile spikelet number per spike (FSN), total spikelet number per spike (TSN), spikelet compactness (SC) and grain number per spikelet (GSP) in the "MD01W233-06-1 \times SS8641" doubled haploid population evaluated in five field trials from 2013 to 2014.

Trait	Chr^{\dagger}	Position [†]	Interval [†]	Chr [‡]	Position [‡]	Interval [‡]	AA§	E1¶	E2¶	E3¶	E4¶	E5¶	$h^{2}(aa)^{\#}$	$h^2(aae)^{\dagger\dagger}$
SL	1A	0	Xwmc496-Xsnp1970 ^{‡‡}	5A	78.9	Xsnp4167-Xsnp3760	0.07***						2.0%	0.2%
SL	5A	78.9	Xsnp4167-Xsnp3760	2D	118.5	Xsnp2795-Xsnp708 ^{‡‡}	-0.04**						0.9%	0.2%
SL	5A	78.9	Xsnp4167-Xsnp3760	5D	44.1	Xsnp4178-Xgdm136 ^{‡‡}	0.07***						2.3%	0.0%
SL	2D	28.5	Xsnp2875-Xsnp2850	2D	118.5	Xsnp2795-Xsnp708§	0.05***						0.6%	0.1%
SL	3A	148.9	Xsnp2968-Xsnp443	3A	58.8	Xsnp4745-Xsnp4774	-0.07***						3.1%	0.4%
SL	3B	93.1	Xsnp3345-Xsnp3289	3B	64.2	Xsnp3737-Xsnp3751	0.07***						2.9%	0.2%
SSN	3A	169.8	Xsnp2983-Xsnp2990 ^{‡‡}	2B	69	Xsnp2591-Xsnp2569	-0.05***						1.0%	0.1%
SSN	1A	51.3	Xsnp1862-Xsnp1823	2D	101.7	Xsnp179-Xsnp2790 [§]	-0.07***						2.5%	0.3%
SSN	5A	1	Xsnp3874-Xsnp3872 ^{‡‡}	1B	87.1	Xsnp2091-Xsnp2052	0.01	0.07*					0.0%	1.4%
SSN	7A	169.4	Xwmc273-Xsnp4655	5D	0	Xsnp4177-Xsnp4179	-0.08***						2.6%	0.2%
FSN	1A	0.9	Xsnp1970-Xbarc28 ^{‡‡}	5D	28.1	Xsnp4178-Xgdm136 ^{‡‡}	0.10***						1.8%	0.0%
FSN	2A	44.8	Xsnp2448-Xsnp2475 ^{‡‡}	3A	173.9	Xsnp2990-Xsnp2905 ^{‡‡}	0.08***						0.7%	0.2%
FSN	3A	173.9	Xsnp2990-Xsnp2905 ^{‡‡}	5D	28.1	Xsnp4178-Xgdm136 ^{‡‡}	-0.12***						0.6%	0.3%
FSN	1A	38.7	Xsnp1993-Xsnp1316	6D	60.4	Xsnp4482-Xsnp814	0.12***				-0.12**	0.10*	1.6%	0.9%
FSN	1B	137.2	Xsnp2067-Xsnp2127	2B	88.3	Xsnp2668-Xsnp2696	0.21***						4.9%	0.3%
TSN	2B	49.8	Xsnp2323-Xsnp768	2D	119.4	Xsnp708-Xsnp1745 ^{‡‡}	-0.08**						0.3%	0.2%
TSN	5B	81.9	Xsnp4050-Xsnp4020	1D	52.6	Xsnp2244-Xsnp2229 ^{‡‡}	-0.11***						0.8%	0.0%
TSN	2D	34.4	Xsnp2850-Xsnp2862 ^{‡‡}	2D	119.4	Xsnp708-Xsnp1745 ^{‡‡}	0.15***						1.3%	0.1%
SC	6A	0	Xsnp4296-Xsnp4276	5B	103.2	Xsnp4086-Xsnp4089	0.02***						2.0%	0.0%
GSP	7A	15.5	Xsnp4718-Xsnp4759	5B	12.2	Xsnp48-Xsnp4152	0.05***						4.2%	0.4%

† The flanking markers, chromosome and position of the first interval involved in the epistasis.

[‡] The flanking markers, chromosome and position of the second interval involved in the epistasis.

[§] The additive × additive effect.

¶ The epistasis × environment effect at each environment. E1: Clarksville 2013; E2: Clarksville 2014; E3: Queenstown 2013; E4: Queenstown 2014;

The heritability estimate for additive × additive interaction effects across five environment.

†† The heritability estimate for epistasis × environment interaction effects across four field trials.

‡‡ Interval with significant additive effect.

* Significantly different from zero at the 0.05 probability level

**Significant different from zero at the 0.01 probability level

** *Significant different from zero at the 0.001 probability level

Discussion

There are very few QTL mapping studies on wheat spike characteristics that integrate additive, epistasis, additive \times environment interaction, and epistasis \times environment interaction effects. In this study, I evaluated a soft red winter wheat DH population to identify QTLs influencing six spike traits and to investigate their interactions.

QTLs for spike characteristics

In the present study, major QTLs for SL, FSN, TSN, and GSP were co-localized and clustered in the 5cM- region on chromosome 1A in three marker intervals: Xwmc496-Xsnp1970, Xsnp1970-Xbarc28 and Xbarc28-Xsnp2005. In previous studies, Xbarc28 was also found to flank QTLs for spike length that explained 10.8% of the phenotypic variation (Marza et al., 2006). Similarly, QTLs for canopy temperature (Shukla et al., 2014), QTLs for pre-harvest sprouting (Munkvold et al., 2009) and QTLs and meta-QTLs for yield components (Zhang et al., 2010) have also been detected in this region. These results indicate the existence of large-effect genes in this interval and thus, high resolution mapping would be recognized to determine if the effects are due to pleiotropy or closely linked QTLs. Five QTLs for SL were identified on chromosomes 5A. Among them, two QTLs with large effects, OSl.cz-5A.1 and OSl.cz-5A.2, overlapped at Xsnp3789. At 10 cM downstream were OSl.cz-5A.2 and OSl.cz-5A.3. QTL OSl.cz-5A.5 was at the distal end of the long arm of 5A. Previous studies have reported vernalization response genes (Vrn genes) and the major wheat domestication gene Q on chromosome 5A (Kato et al., 1998). Vrn genes together with photoperiod response genes (*Ppd* genes) and earliness per se genes (*Eps* genes)

determine flowering time of wheat and hence, in part, confer wheat wide adaptation to diverse regions around the world (Snape et al., 2001). The Q gene is a well-known domestication locus conferring the free-threshing character and is responsible for many other domestication-related traits such as rachis fragility, glume shape and tenacity, spike length, plant height, and spike emergence time (Faris et al., 2003; Simons et al., 2006; Sormacheva et al., 2014). The five SL QTLs on chromosome 5A were in the same regions where Vrn-A1 and Q are located. Diagnostic markers will be employed to further verify the existence of Vrn-A1 and Q in this DH population. QTL fine mapping is also necessary to determine if one or both of these two genes contributed to SL in this study and if new locus other than Vrn-A1 and Q was detected. Additionally, consistent QTLs for SL (OSl.cz-3B.2 and OSl.cz-3B.3) were identified on chromosome 3B in E1, E2, E4, and E5. *QSLcz-3B.2* and *QSLcz-3B.3* overlapped at locus Xsnp3335 and were located in a region harboring QTLs for FSN, TSN, and GSP. In the same region, Li et al. (2007b) detected QTLs for grain yield and grain number per spike in two environments using a population of recombinant inbred lines derived from two winter wheat cultivars. Wang et al. (2009) also found this region significant for grain filling rate and yield-related traits over multiple environments. Three QTLs on 2D (Table 4.4) were of special interest because these were the only three loci where MDW233 alleles were associated with a longer spike. In a QTL mapping study for spike-related traits, Ma et al. (2007b) detected two QTLs on chromosome 2B flanked by marker Xgwm261 for SL and SC in the cross of winter genotypes Nanda 2419 and Wangshuibai where the QTLs linked to Xgwm261 explained 8.8 to 23.2% of the phenotypic variation. In my study, Xgwm261 was 2.3

cM and 13.3 cM away from *QSl.cz-2D.1/QFsn.cz-2D.1* and *QSl.cz-2D.2*, respectively. In addition, *Xgwm261* was reported to flank co-localized QTLs and a QTL cluster for yield related traits including plant height, harvest index, days to maturity, thousand grain weight, and grain weight per spike (Mason et al., 2013). These results suggest that these regions on chromosome 2D may be the same. Furthermore, *QSl.cz-2D.3* mapped to the long arm of chromosome 2D and shared the same interval with major QTL *QFsn.cz-2D.3* and *QTsn.cz-2D.4* which coincided with the QTLs for FSN and TSN in Ma et al. (2007). The same position and genetic effects suggested the possibiligy of similar underlying QTLs.

A few studies have documented QTLs/genes for SSN, FSN, and TSN (Cui et al., 2012; Ma et al., 2007b). Some previously reported QTLs were confirmed in the present study. A minor QTL, *QSsn.cz-6D*, is consistent with the QTL detected by Cui et al. (2012) who also located a cluster of QTLs for spike characteristics on chromosome 2B corresponding with the major QTL clusters identified in the present study. QTLs in this cluster were repeatedly detected in almost all environments evaluated. At these loci, SS8641 contributed positive additive effects for SSN, TSN, and SC, whereas MDW233 was associated with positive GSP suggesting that the SS8641 allele of this cluster may lower spikelet fertility and increase TSN and SC by increasing the number of sterile spikelets. The SS8641 allele of this region should be avoided in breeding programs. In addition, a QTL cluster for FSN and TSN was identified on chromosome 5D flanked by *Xsnp4156-Xgdm136* and was located in the

(2012). Cuthbert et al. (2008) reported a QTL cluster for grain numbers per spike, grain yield, thousand grain weight, grain filling time, and days to heading on chromosome 2D which may correspond to the region of major QTL OSsn.cz-2D.3 identified in this study (Table 4.4). At the distal end of chromosome 2D, I detected three closely linked QTLs QFsn.cz-2D.4, QTsn.cz-2D.5, and QGsp.cz-2D. These QTLs were not located at the region of the *compactum* (C) locus, a spike-compacting gene on the long arm of chromosome 2D (Johnson et al., 2007a). The SS8641 alleles in this region decreased FSN and TSN but increased GSP. The association of this region with spike traits has not been reported elsewhere. Furthermore, I found that the major QTL QFsn.cz-2D.2 shared the interval with QTsn.cz-2D.2 and QSsn.cz-2D.1 and overlapped with QSn.cz-2D.2 and QTsn.cz-2D.3 at the locus Ppd-D1. The effects of these QTLs were possibly caused by the locus *Ppd-D1* which is a member of the *Ppd1* genes known to confer photoperiod sensitivity and influence agronomic traits such as plant height, days to heading and thousand grain weight (Guo et al., 2010). Recently, the *Ppd-D1* locus was shown to control photoperiod-dependent floral induction and that it has a major inhibitory effect on paired spikelet formation by regulating the expression of the FLOWERING LOCUS T (FT) (Boden et al., 2015).

The QTL cluster on chromosome 5A for SC included the locus Xgwm304 that is neither close to the Q gene nor the Vrn-A1 gene but it has been related to grain yield and thousand grain weight by Cuthbert et al. (2008) and SL and SC by Ma et al. (2007b). In these two studies, this region was identified as harboring major QTLs because of high PVE values similar to my results. Thus, it is possible that this region may contribute to grain yield by increasing spikelet numbers and grain weight. Sourdille et al. (2003) used a DH population derived from the cross Courtot \times Chinese Spring to study wheat development traits and detected one QTL on the long arm of chromosome 5D for SC. This QTL explained 13.6% of the phenotypic variation and was similar to the genomic region *Xsnp876-Xsnp4157* where two major QTLs for SL and SC were identified in the present study. Another QTL cluster comprising of four major QTLs for GSP on chromosome 5B (Table 4.4) coincided with the interval of the SL QTL *QSl.ccsu-5B.2* identified by Kumar et al. (2007).

Chromosome 3A of wheat is known to contain QTLs for grain yield and other important agronomic traits. Using a recombinant inbred line population derived from the winter wheat cultivar Cheyenne (CNN) and its single chromosome substitution line CNN (WI3A) where chromosome 3A of CNN was substituted for Wichita (WI) chromosome 3A, Mengistu et al. (2012) and Dilbirligi et al. (2006) detected QTLs for grain yield, plant height, spikes per square meter, and grain number per spike and found that most of the detected QTLs on 3A were co-localized in two regions. In the present study, I detected five QTLs on chromosome 3A for SC and SSN among which *QSsn.cz-3A.1* explained 13.8% of the phenotypic variation while the rest were minor QTLs. Based on the mapping positions of SSR markers used in the current and previous studies (Somers et al., 2004), these five QTLs were similar to the QTLs previously identified by Dilbirligi et al. (2006) and Mengistu et al. (2012).

Genetic complexity of spike characteristics

Most important agronomic traits are quantitative in nature controlled by polygenes and influenced by the environment. Understanding the genetic and environmental factors causing the phenotypic variation of quantitative traits is essential for the genetic improvement of crops via knowledge-based breeding (Mackay, 2001; Würschum, 2012). In the present study, the effects of major, minor, and epistatic QTLs as well as their interactions with the environment and their relative contributions to spike characteristics were estimated (Figure 4.2). The QTLs with additive effects were the largest in total number and had the largest genetic contribution to phenotypic variation. This agreed with previous QTL studies involving epistasis, Q×E and QQ×E interactions (Kuchel et al., 2007a; Wu et al., 2012; Xing et al., 2002; Zhang et al., 2014). In addition, QTLs for spike characteristics were not evenly distributed within and across chromosomes and tended to cluster (Figure 4.1). I identified QTL clusters on chromosome 1A, 5A, 2B, 3B, 5B, 1D, 2D, and 5D where QTLs for multiple spike characteristics were colocalized or closely linked within a 10-cM region. In most cases, each cluster contained at least one major QTL. The clustering of QTLs also partially explained the correlation between spike characteristics. In this study, SL was highly correlated with FSN across environments (Table 4.3). This could be caused by the co-localization of OSl.cz-1A and OFsn.cz-1A plus the effects of closely linked QTLs OSl.cz-3A.1, OSl.cz-3A.2 and OFsn.cz-3A.1. Despite of the slight difference in interpretation, characterizing the interaction at two or more loci or epistasis is as important in quantitative genetics as in classical genetics. I found that interactions ($Q \times E$, $Q \times Q$ and

 $QQ \times E$) served as modifiers for spike characteristics determination in my DH population. For example, the interval Xsnp4167-Xsnp3760 on chromosome 5A was not detected with significant additive effects but contributed to SL through its interactions with Xsnp2795-Xsnp708, Xwmc496-Xsnp1970, and Xsnp4178-Xgdm136, which were associated with significant additive effects for FSN, GSP, and SL, respectively. Significant epistasis was also detected between non-significant intervals such as Xsnp2067-Xsnp2127 and Xsnp2668-Xsnp2696 which increased FSN and accounted for 4.9% of the phenotypic variation. Similar results were reported by Ma et al. (2007b) where the interaction of two non-significant loci on chromosome 3D decreased TSN and FSN. These results confirmed that loci without main effects may contribute to trait determination through epistasis (Li et al., 2001). Additionally, I found that the SS8641 allele at the interval Xsnp1970-Xbarc28 increased FSN and TSN in E5 and these effects was enhanced by 21.5% through the Q×E interaction. Although the effects and contribution from $Q \times E$, $Q \times Q$ and $QQ \times E$ interactions were relatively smaller compared to additive main effects, they were important terms finetuning the expression of spike traits. This is valuable information for pyramiding QTLs in breeding programs.

Conclusion

Spike characteristics determine the number of grains produced on each spike. Genetically improving grain number per spike is widely accepted as one of the key paths towards higher grain yield. In this study, QTL mapping in a bi-parental population was performed and detected a total of 109 QTLs among which consistent QTLs such as *QSl.cz-1A* or *QFsn.cz-1A* for SL and FSN, *QGsp.cz-2B.1* for GSP, and

QSc.cz-5A.3 for SC, explained up to 30.9%, 15.6%, and 80.2% of the phenotypic variation, respectively. I also found that the average contribution of *QFsn.cz-1A* to FSN at each trial was enhanced by 19% via interaction with the interval *Xsnp4178-Xgdm136*. In addition, QTLs clusters on chromosomes 1A, 5A, 2B, 3B, 5B, 1D, and 5D with synergistic or antagonistic genetic effects partially explained the phenotypic correlation between spike traits. These results provide valuable information for manipulating spike morphology for breeding purposes.

Chapter 5: Multivariate analysis of grain yield and yield related traits in a doubled haploid population of soft red winter wheat

<u>Abstract</u>

To study the interrelationships among grain yield and yield contributing traits, a series of statistical analyses including correlation, multiple linear regression, cluster analysis, principal component analysis and structural equation modeling were conducted in a soft red winter wheat doubled haploid population derived from the cross MD01W233-06-1 by SS8641. Six structural equation models with feedback loops were constructed and showed that spikes per square meter had the highest positive contribution to grain yield followed by grain weight per spike and that grains per spikelet and fertile spikelet number per spike were compensatory targets that mediate yield component compensation. In addition, DH84 and DH96 which yielded 24.13% and 22.64% higher than the mean performance of the whole population, respectively, may have potential as new cultivars.

Introduction

Wheat (*Triticum aestivum* L.) is one of the most important food crops, occupying 17% of the world's crop acreage, feeding about 40% of the world's population and providing 20% of total food calories and protein in human nutrition (Gupta et al., 2005). Continuous genetic improvement of wheat yield potential via breeding is essential to securing a stable food supply. In a wheat breeding program, a breeder usually records a number of agronomic characters on which statistical analyses are made to get a better understanding of the germplasm. The information is then utilized to make selections. Therefore, analytical methods that can extract the most

information from large datasets and provide insights into the nature and magnitude of association of plant traits are needed, especially when clear experimental control of the inter-correlated traits is difficult.

Several statistical methods have been utilized to investigate wheat grain yield and its related characters. For example, phenotypic correlation analysis is an important way to evaluate the association between plant characters. However, simple correlation does not necessarily imply a cause-and-effect relationship. The observed correlation could be due to unknown environmental or genetic factors. Genetic correlation is a measure of the extent to which plant characters are associated at the genetic level (Waitt and Levin, 1998) and is used as a supplement to phenotypic correlation when making selection decisions (Holland, 2006). Alternatively, multiple regression analysis can be useful when the main interest is the prediction of the response variable from a set of predictor variables or to select candidate variables for further analyses. Using multiple linear regression analysis, Leilah and Al-Khateeb (2005) reported that grain weight per spike, harvest index, biological yield, spike number per square meter and spike length were major contributors to wheat grain yield. Additionally, cluster and principal component analyses are often used separately or combined to group cultivars or agronomic variables into main groups or subgroups based on similarity, which is also useful for parental selection in breeding programs and crop modeling (Khodadadi et al., 2011; Leilah and Al-Khateeb, 2005). Furthermore, path analysis divides the correlation coefficients into direct and indirect effects and has been employed to study yield formation in cereal crops by separating the direct influence of each yield component on grain yield from the indirect effects caused by mutual relationships among yield components themselves (Kashif and Khaliq, 2003; Li et al., 2006; Moral et al., 2003). Most path analysis studies on yield formation, however, have two main general limitations: 1) researchers assume bidirectional causal pathways between yield components and yield related traits; and 2) grain yield is modeled as a resultant variable and all other traits as causal variables with direct path toward grain yield (Kashif and Khaliq, 2003; Li et al., 2006). Additionally, whether a yield component can influence others that develop earlier is questionable given that yield components develop sequentially (Dofing and Knight, 1992). Furthermore, path analysis assumes that all variables are measured without error and that no correlation between the error terms and causal loops exist (Meehl and Waller, 2002).

Structural equation modeling (SEM) is a powerful multivariate approach to model complex relationships between latent and measured variables while accounting for measurement error (Ullman, 2006). SEM is an extension of general linear modeling (GLM) procedures, such as the ANOVA and multiple regression analysis. Its main goal is to determine if a specified theory about the causal pattern of multiple inter-correlated variables, usually represented by a path diagram, is consistent with empirical data. This consistency is evaluated through data-model fit indices that measure the extent to which the proposed network of relations is plausible. Four most commonly used fit indices are 1) standardized root mean squared residual (SRMR), 2) root mean squared error of approximation (RMSEA), 3) normed fit index (NFI),

and 4) nonnormed fit index (NNFI) (Hooper et al., 2008). Similar to classic path analysis, SEM is capable of conveying casual relationships among mutually intercorrelated dependent and independent variables (Kline, 2011). One of the primary advantages of SEM (vs. other applications of GLM such as ANOVA and path analysis) is that less restrictive assumptions exist in SEM which makes SEM a popular confirmatory and exploratory approach in social sciences (Marsh et al., 2014). SEM has been adapted to the quantitative genetics mixed-effects models settings by Gianola and Sorensen (2004) and promoted by Lamb et al. (2011) in plant sciences to study yield components, complex multi-site field trails etc. However, no applications have been reported in major crop plants.

The present study was undertaken to investigate and model the phenotype network regarding wheat grain yield formation through multivariate analyses. The novelty of this research is twofold: 1) it provides an overall view on grain yield formation by including yield components, spike morphology and plant architecture traits and 2) it introduces SEM as a supplement to traditional multivariate approaches to resolve the interrelationships among yield contributing traits. Data used in this study was collected at the end of growing seasons and, thus, phenotype network constructed in this study did not represent dynamic regulating network or mimic any developmental processes.

Materials and Methods

Field trials and data collection

Data used in this chapter was collected from a doubled haploid population of soft red winter evaluated in five field environments (refer to the chapter 2, 3, and 4 of this dissertation for details).

Statistical analyses

Phenotypic correlation analysis was performed by PROC CORR procedure of SAS, Version 9.3 (SAS Institute, Cary, NC 2013). Genetic correlation coefficients were estimated using MANOVA method (Liu et al., 1997) by PROC GLM procedure of SAS. Multiple linear regression and stepwise multiple linear regression was conducted using PROC REG procedure of SAS. Cluster analysis (using standardized data and Ward method) and principal component analysis (using correlation matrix and REML method) were performed by JMP[®] Pro, Version 11 (SAS Institute, Cary, NC, 2014). Structural equation modeling was based on correlation matrix and performed using LISREL, Version 9.1 (Joreskog and Sorbom, 2012).

Results and Discussion

Phenotypic and genetic correlation analyses

According to quantitative genetics theory, genetic and environmental causes of correlation combine together to produce phenotypic correlations. The magnitude and sign of phenotypic and genetic correlations, however, are not necessarily related (Waitt and Levin, 1998). It is important to know for breeders if the phenotypic correlation is due to heritable genetic factors or external environmental conditions. In

this study, a matrix of pairwise phenotypic and genetic correlation coefficients were computed and are presented in Table 5.1. GYLD was positively associated with SPSM and TGW but was negatively correlated with FLL, FLW, FLA, SL, FSN, TSN, and HD. SPSM and TGW had the highest positive phenotypic and genotypic association with GYLD implying that improving these traits could result in higher grain yield and this effect would be highly heritable. A significant positive correlation between GWPS and GYLD was not found in pooled correlation analysis but was detected in two environments: E4 and E5, which was similar with the results reported by Marza et al. (2006) and Heidari et al. (2011). The negative correlations between GYLD and FLL, FLW, FLA, SL, FSN, TSN, and HD suggested that early heading genotypes with smaller flag leaves, shorter spikes, and less fertile spikelets, and thus with lower grain number and lighter grain weight would contribute to higher grain yield. This was true in E1, E2, E3, and E4 where these unfavorable traits were compensated by higher SPSM but not in E5 where the compensation from SPSM was not enough, probably due to higher temperatures during the growing season. In a study to evaluate wheat yield formation under Mediterranean conditions, Moral et al. (2003) reported that durum wheat yielded less in warmer environments than in cooler regions mainly due to reduced SPSM and TGW. Similarly, Hou et al. (2012) found that winter wheat grew faster and produced more tillers but tended to decrease SPSM under warmer conditions also resulting in lower grain yield.

Cluster and principal component analysis

Cluster analysis has been used to classify wheat ecotypes and to evaluate genetic diversity in wheat germplasm collections. Cluster analysis groups genotypes into

clusters where genotypes in the same cluster exhibit high homogeneity but have high heterogeneity among clusters. In this study, I clustered the 124 DH lines into five clusters (Figure 5.21~5.26). Membership of each line is presented in Appendix D. The means of dendrogram clusters at each environment are presented in Table 5.6. The cluster with the highest grain yield at each environment was consistently associated with higher SPSM, smaller FLA, less GPS, lighter GWPS, shorter SL, fewer FSN and TSN, which also agreed with the results from phenotypic and genetic correlation analysis of this study.

Principal component analysis (PCA) is a standard multivariate technique for complex dataset analysis where observations are described by multiple inter-correlated variables. Its objective is to extract the most important information from the original inter-correlated variables by maximizing the variance of a set of new orthogonal variables called principal components, and to display the pattern of similarity of the observations and of the variables in maps (Abdi and Williams, 2010). Principal components are linear combinations of original variables. The first principal component has the maximal variance. The second principal component has maximal variance in a direction orthogonal to the first principal component, and so on. In this study, PCA grouped the investigated wheat variables into five main components explaining more than 80% of the total variation (Table 5.4). Specifically, the first two principal component accounted for 30.6%, 27.1%, 32.5%, 30.7%, 34.5%, and 33.1% of the total variation and second principal component for 20.2%, 18.1%, 22%, 18.7%,

and 23.7% of the total variation at E1, E2, E3, E4, and E5 trials, respectively. The first principal component was related to yield components and yield contributing traits whereas the second principal component was related to vegetative growth and spikelet fertility across trials (Table 5.5). The traits with largest loadings to the first principal component were GWPS, GPS, SPSM, SL and FSN, suggesting these were indicative of yield potential. The first two principal components and wheat variables were plotted in biplots (Figure 5.1). From the biplots, vectors representing uncorrelated traits formed right angles (90°) (e.g. GPS vs. HD, SSN vs. FSN), whereas highly correlated traits formed either acute (positive correlation; e.g. SPSM vs. GYLD) or obtuse (negative correlation; e.g. GYLD vs. FLA) angles. In general, three observations were made from the biplots: 1) SPSM and TGW were mostly positively associated with GYLD, 2) SSN, SC, GSP, and FLS were independent of GYLD, 3) HD, FLW, FSN, FLA, FLL, and GPS were negatively associated with GYLD. GWPS showed a slightly positive to no correlation with GYLD, which agreed with the results of previous phenotypic correlation analyses.

Additionally, cluster analysis coupled with PCA was used to select high yielding DH lines in this study. The first two principal components from each environment were plotted with DH cluster membership as labels (Figure 5.21~5.26). At E1, the highest yielding cluster (Cluster 1) was separated from the lowest yielding cluster (Cluster 4) as was Cluster 2 from Cluster 4 at E2, Cluster 5 from Cluster 3 at E3, Cluster 1 from Cluster 4 at E4, and Cluster 1 from Cluster 4 at E5. The extracted principal components were able to distinguish different clusters and, thus, largely confirmed

the generated cluster membership. Two DH lines, DH96 and DH84, stayed in the highest yielding clusters across all five environments. Furthermore, when data from the five environments were averaged, DH96 and DH84 ranked second and third among all lines, increasing grain yield by 24.13% and 22.64% respectively. Thus, DH96 and DH84 could be candidates to be new cultivars with a stable performance across these environments.

Multiple linear regression analysis

Regression coefficients and the associated probability values for each variable in predicting wheat grain yield are presented in Table 5.2 and 5.3. The final models from stepwise linear regression analyses explained more than 95% of the total variation in grain yield. Although the variables remaining in the models varied at different environments, GWPS and SPSM were shared by all, suggesting the importance of SPSM and GWPS as selection criteria in wheat breeding for grain yield. Similarly, Leilah and Al-Khateeb (2005) also observed that SPSM and GWPS were the most effective variables influencing wheat grain yield.

Structure equation modeling (SEM)

Phenotypic traits can have causal effects on each other (Rosa et al., 2011). Information regarding phenotype networks describing the cause-and-effect relationships and feedback between traits is very helpful to predict the performance of biological systems. In this study, a phenotype network regarding grain yield and yield contributing traits was modeled under the frame of SEM. The purpose was to quantify the relative contributions of correlated causal sources of variation once a certain network of interrelated variables with biological significance has been accepted (Shipley, 2004). Initial models were constructed separately for grain yield and yield components and spike characteristics based on the results obtained from previous multivariate analyses and published results on the interrelationships among grain yield and yield contributing traits (Dofing and Knight, 1992; Moral et al., 2003). The initial models were then integrated into one. I included paths from GPS and TGW to GYLD at my first attempt to integrate initial models. The path coefficients were not significant and overall model fitting failed although this seemed meaningful biologically. LISREL suggested a list of paths that could improve fit indices. Based this list, the modification of paths was performed to obtain the best combination of four fit indices. Final models are shown in Figure 5.3.

All the path coefficients in the phenotype network were highly significantly different from zero (Figure 5.3). Across six models, GWPS and SPSM had direct causal influence on GYLD. The loadings for the path from SPSM to GYLD were higher than that for the path from GWPS suggesting that SPSM had a relatively more direct contribution to GYLD. No direct contribution from GPS or TGW to GYLD was established. However, GPS and TGW had an indirect effect on GYLD via GWPS. Additionally, FSN and GSP were feedback targets where depressing effect from GWPS, SPSM, TGW and GYLD were observed. GSP had more feedback effect than FSN. Previous studies found that SPSM had a direct negative effect on GPS and TGW (Moral et al., 2003) and that this compensation arose from the fact that these traits develop sequentially with later-developing traits under control of earlierdeveloping ones (Slafer, 2007). However, in this study, a direct negative effect on GWPS from SPSM was significant only in Clarksville 2014 and Queenstown 2014. Although a direct path from SPSM to GWPS was absent in the other three trials, SPSM negatively affected GWPS by depressing GSP and FSN and hence GPS (Figure 5.3) suggesting GSP and FSN as mediators in yield component compensation. To my knowledge, this is the first report of GSP and FSN as direct feedback regulating targets in wheat.

Direct genetic evidence of feedback paths in SEM

The results of the QTL analyses of the set of agronomic traits involved in the present study (Chapter 2, 3, and 5 of this dissertation) were used to evaluate the validity of feedback paths in the structural equation models at each trial. The feedback path from SPSM to GSP in the model at Clarksville 2013 and Queenstown 2013 could be partially explained by the interval Xwmc496-Xsnp1970 where QTL OSsm.cz-1A.1 and QTL QGsp.cz-1A.1 co-localized and the interval Xbar28-Xsnp2005 where QTL QSsm.cz-1A.3 and QTL QGsp.cz-1A.2 also co-localized. The MDW233 allele at these two loci increased SPSM but decreased GSP. The feedback path from GYLD to GSP in the model at Clarksville 2014 could be associated with the region Xsnp3382-Xsnp3368 on chromosome 3B where QTLs with opposite genetic effects on GYLD and GSP were located closely. The feedback path from GYLD to FSN in the model at Clarksville 2013 could be supported by the genomic region Xwmc496-Xbar28 on chromosome 1A where QTL QGld.cz-1A and QTL QFsn.cz-1A co-localized but showed opposite genetic effects on GYLD and FSN. Another genetic evidence might be the interval Xsnp2862-XPpd1 on chromosome 2D where its SS8641 allele

increased grain yield but decreased FSN. Additionally, the interval *Xsnp1970-Xbar28* on chromosome 1A and *Xsnp3389-Xsnp3344* on chromosome 3B may be the underlying genetic factors for the feedback path from **SPSM to FSN** in the model at Kinston 2014, where the MDW233 allele increased SPSM but decreased FSN. No QTLs were found to directly support the feedback paths from **GWPS to GSP and FSN** and from **TGW to FSN**. This could be due to two reasons: 1) the threshold level set to detect a significant QTL was too high so that QTLs with minor effects were overlooked. A consequence of this is that researchers would miss QTLs that could explain the feedback paths and 2) the causal relations could be due to methylation quantitative trait loci (meQTLs) in addition to DNA sequence changes (Koch, 2014) which are not detected in conventional QTL analyses.

Conclusion

Multivariate analyses were used to construct a phenotype network involving grain yield and yield related traits. Results showed that SPSM (spikes per square meter) was the most important trait that directly and positively contributed to grain yield followed by GWPS (grain weight per spike). In addition, GPS (grains per spike) had more weight on GWPS (grain weight per spike) than TGW (thousand grain weight) and GSP (grains per spikelet) had more weight on GPS (grains per spike) than FSN (fertile spikelet number). Therefore, high SPSM and GSP and moderate TGW and FSN could be the targets for breeding for higher grain yield in the Mid-Atlantic region.

Table 5.1 Genotypic (r_g) and phenotypic (r_p) correlation coefficients among the grain yield and yield contributing traits in the MD01W233-06-1 × SS8641 doubled haploid population. r_p is shown in the upper triangular and r_g in the lower triangular. Traits evaluated include grain yield (GYLD), grains per spike (GPS), grain weight per spike (GWPS), spikes per square meter (SPSM), and thousand-grain-weight (TGW), plant height (PHT), flag leaf length (FLL), flag leaf width (FLW), flag leaf area (FLA), flag leaf shape (FLS), spike length (SL), sterile spikelet number per spike (SSN), fertile spikelet number per spike (FSN), total spikelet number per spike (TSN), spike compactness (SC), grain number per spikelet (GSP), and dates to heading (HD). r_g and r_p were estimated from all five trials' data. Significance was not tested for r_g .

	GYLD	GPS	GWPS	SPSM	TGW	PHT	FLL	FLW	FLA	FLS	SL	SSN	FSN	TSN	SC	GSP	HD
GYLD		-0.17	0.12	0.70***	0.37***	0.13	-0.25**	-0.43***	-0.41***	0.09	-0.24**	-0.14	-0.40***	-0.44***	-0.15	0.11	-0.46***
GPS	-0.15		0.66***	-0.58***	-0.38***	0.06	0.45***	0.19*	0.40***	0.26**	0.49***	-0.36***	0.71***	0.51***	-0.06	0.76***	0.03
GWPS	0.14	0.66		-0.60***	0.36***	0.29***	0.36***	0.16	0.33***	0.21*	0.56***	-0.25**	0.41***	0.28**	-0.36***	0.56***	-0.24***
SPSM	0.69	-0.59	-0.63		0.02	-0.11	-0.45***	-0.45***	-0.56***	-0.08	-0.56***	0.07	-0.58***	-0.52***	0.13	-0.30***	-0.19*
TGW	0.36	-0.37	0.38	-0.01		0.36***	-0.11	0.02	-0.05	-0.12	0.08	0.21*	-0.35***	-0.24***	-0.34***	-0.24**	-0.29**
PHT	0.08	0.08	0.31	-0.17	0.33		0.24**	-0.21*	0.04	0.37***	0.12	0.18*	-0.01	0.07	-0.07	0.07	0.01
FLL	-0.36	0.47	0.40	-0.57	-0.10	0.27		0.31***	0.82***	0.66***	0.42**	0.19*	0.45***	0.50***	0.02	0.22*	0.36***
FLW	-0.59	0.17	0.20	-0.59	0.08	-0.23	0.30		0.79***	-0.51***	0.30***	0.18*	0.39***	0.45***	0.09	-0.09	0.54***
FLA	-0.57	0.40	0.38	-0.72	-0.01	0.05	0.82	0.80		0.12	0.45***	0.23*	0.52**	0.59**	0.06	0.09	0.55***
FLS	0.12	0.28	0.20	-0.07	-0.15	0.41	0.65	-0.52	0.10		0.16	0.01	0.11	0.10	-0.06	0.27**	-0.11
SL	-0.30	0.47	0.56	-0.62	0.12	0.13	0.45	0.31	0.48	0.17		-0.03	0.65***	0.60***	-0.58***	0.10	0.08
SSN	-0.26	-0.38	-0.27	-0.02	0.23	0.20	0.21	0.17	0.23	0.04	-0.02		-0.09	0.34***	0.38***	-0.47***	0.51***
FSN	-0.42	0.69	0.42	-0.61	-0.31	-0.03	0.47	0.44	0.57	0.09	0.64	-0.12		0.90***	0.15	0.09	0.35***
TSN	-0.51	0.49	0.28	-0.59	-0.20	0.06	0.54	0.49	0.64	0.10	0.61	0.32	0.90		0.30***	-0.11	0.55***
SC	-0.13	-0.08	-0.39	0.16	-0.34	-0.09	-0.01	0.10	0.05	-0.09	-0.62	0.33	0.10	0.24		-0.22*	0.46***
GSP	0.15	0.78	0.55	-0.29	-0.26	0.11	0.22	-0.15	0.06	0.31	0.07	-0.47	0.09	-0.12	-0.20		-0.28**
HD	-0.58	0.02	-0.25	-0.27	-0.29	-0.01	0.41	0.61	0.63	-0.12	0.12	0.47	0.39	0.58	0.41	-0.31	

* Significant at 0.05 probability level

** Significant at 0.01 probability level

*** Significant at 0.001 probability level

Table 5.2 Multiple linear regression of the MD01W233-06-1 × SS8641 doubled haploid population. Grain yield (GYLD) as dependent variable and grains per spike (GPS), grain weight per spike (GWPS), spikes per square meter (SPSM), and thousand-grain-weight (TGW), plant height (PHT), flag leaf length (FLL), flag leaf width (FLW), flag leaf area (FLA), flag leaf shape (FLS), spike length (SL), sterile spikelet number per spike (SSN), fertile spikelet number per spike (FSN), spike compactness (SC), grain number per spikelt (GSP), and heading date (HD) as independent variables. Total spikelet number per spike (TSN) was not included in the analysis because of its multicollinearity with SSN and FSN. Estimates of regression coefficients and the associated p values are shown.

	Clarksville 2013		Clarksville 2014		Queenstown 2013		Queenstown 2014		Kinston	2014 [†]	Overall	
Variable	Estimate	P value	Estimate	P value	Estimate	P value	Estimate	P value	Estimate	P value	Estimate	P value
Intercept	-1233.71	0.0213	-520.30	0.2398	221.20	0.5448	-994.20	<.0001	-232.08	0.3173	-188.71	0.6140
GPS	-13.60	0.0472	-10.51	0.0213	1.28	0.5790	-13.96	<.0001	-2.15	0.5470	-9.94	0.0340
GWPS	412.69	<.0001	767.35	<.0001	484.42	<.0001	483.40	<.0001	446.89	<.0001	517.05	<.0001
SPSM	1.19	<.0001	0.93	<.0001	1.29	<.0001	1.05	<.0001	1.10	<.0001	1.08	<.0001
TGW	0.97	0.5116	1.20	0.3731	-0.56	0.6868	2.01	0.0092	0.64	0.4663	1.49	0.3043
PHT	0.83	0.0184	0.05	0.8966	0.05	0.8722	0.46	0.0145			-83.71	0.0132
FLL	23.39	0.2645	8.59	0.6147	5.08	0.7402	20.00	0.0318			32.65	0.0294
FLW	156.64	0.2374	117.05	0.3538	-68.27	0.6104	130.07	0.0648			58.11	0.0051
FLA	-16.81	0.2006	-8.48	0.3928	0.74	0.9313	-13.88	0.0077			-234.26	0.0212
FLS	-2.62	0.8495	1.55	0.9075	-10.10	0.4558	-4.00	0.6037			-0.16	0.5415
SL	-45.07	0.2789	-100.51	0.0319	-87.00	0.0218	-52.81	0.0168	-50.26	0.0380	12.11	0.3927
SSN	16.84	0.3571	39.68	0.0487	25.74	0.1169	17.15	0.1000	16.35	0.1014	-116.24	0.3442
FSN	55.92	0.0164	66.72	0.0030	33.69	0.0585	62.31	<.0001	24.84	0.0949	-0.33	0.9676
SC	-149.28	0.2291	-290.59	0.0411	-240.23	0.0370	-158.32	0.0166	-141.71	0.0524	-14.75	0.2511
GSP	208.35	0.0403	151.10	0.0367	-24.48	0.4378	202.47	<.0001	27.72	0.6457	144.65	0.0406
HD	1.25	0.3804	-0.32	0.8399	-0.59	0.4884	-0.10	0.8936	0.25	0.5540	-0.22	0.8005
R sq	0.9669		0.9620		0.9838		0.9848		0.9827		0.9722	
R sq (adj)	0.9623		0.95	68	0.98	15	0.98	27	0.9812		0.9683	

† PHT, FLL, FLW, FLA, FLS were not evaluated in Kinston 2014.

Table 5.3 Stepwise multiple linear regression of the MD01W233-06-1 × SS8641 doubled haploid population. Grain yield (GYLD) as dependent variable and grains per spike (GPS), grain weight per spike (GWPS), spikes per square meter (SPSM), and thousand-grain-weight (TGW), plant height (PHT), flag leaf length (FLL), flag leaf width (FLW), flag leaf area (FLA), flag leaf shape (FLS), spike length (SL), sterile spikelet number per spike (SSN), fertile spikelet number per spike (FSN), spikelet compactness (SC), grain number per spikelet (GSP), and heading date (HD) as independent variables. Total spikelet number per spike (TSN) was not included in the analysis because of its multicollinearity with SSN and FSN. Variables kept in the final model, their regression coefficients, and the associated p values are shown.

	Clarksville	e 2013	Clarksvill	e 2014	Queenstown	n 2013	Queenstow	/n 2014	Kinston 2	2014†	Overa	all
Variable	Estimate	P value	Estimate	P value	Estimate	P value	Estimate	P value	Estimate	P value	Estimate	P value
Intercept	-613.72	<.0001	-732.93	<.0001	-662.59	<.0001	-599.60	<.0001	-497.80	<.0001	-518.98	<.0001
GPS												
GWPS	436.68	<.0001	769.62	<.0001	475.04	<.0001	493.77	<.0001	430.65	<.0001	520.18	<.0001
SPSM	1.19	<.0001	0.93	<.0001	1.30	<.0001	1.08	<.0001	1.10	<.0002	1.10	<.0001
TGW							1.18	0.0171	0.85	0.0436		
PHT	0.95	0.0031					0.49	0.0131				
FLL												
FLW												
FLA												
FLS												
SL												
SSN					-9.71	0.0083	-7.82	0.0029				
FSN											-4.62	0.0019
SC					25.42	0.0447						
GSP												
HD												
R sq	0.960)7	0.954	5	0.982	5	0.978	33	0.981	16	0.967	76
R sq (adj)	0.959	8	0.953	7	0.981	9	0.977	74	0.981	12	0.966	58

† PHT, FLL, FLW, FLA, FLS were not evaluated in Kinston 2014.

Table 5.4 Principal component analysis of the MD01W233-06-1 \times SS8641 doubled haploid population based on sixteen agronomic traits including grain yield (GYLD), grains per spike (GPS), grain weight per spike (GWPS), spikes per square meter (SPSM), and thousand-grain-weight (TGW), plant height (PHT), flag leaf length (FLL), flag leaf width (FLW), flag leaf area (FLA), flag leaf shape (FLS), spike length (SL), sterile spikelet number per spike (SSN), fertile spikelet number per spike (FSN), total spikelet number per spike (TSN), spikelet compactness (SC), and grain number per spikelet (GSP). Eigen values for each extracted principle component (PC), percentage (Per.) explained by each PC and cumulative percentage (Cum. Per.) are shown.

	Cl	arksville 2	013	Cl	arksville 2	014	Qu	eenstown 2	2013	Qu	eenstown 2	2014	K	Linston 201	4†		Overall	
	Eigen value	Per.	Cum. Per.	Eigen value	Per.	Cum. Per.	Eigen value	Per.	Cum. Per.	Eigen value	Per.	Cum. Per.	Eigen value	Per.	Cum. Per.	Eigen value	Per.	Cum. Per.
PC1	5.21	30.62	30.62	4.61	27.13	27.13	5.52	32.49	32.49	5.22	30.68	30.68	4.14	34.53	34.53	5.62	33.07	33.07
PC2	3.44	20.22	50.84	3.08	18.13	45.26	3.74	21.98	54.46	3.18	18.71	49.40	2.85	23.71	58.24	3.35	19.71	52.78
PC3	2.06	12.13	62.97	2.30	13.55	58.80	1.83	10.74	65.20	2.19	12.88	62.28	1.87	15.57	73.80	2.02	11.87	64.65
PC4	1.70	9.99	72.96	1.98	11.64	70.44	1.55	9.12	74.32	1.73	10.19	72.46	1.36	11.30	85.11	1.85	10.91	75.56
PC5	1.30	7.67	80.62	1.41	8.29	78.73	1.20	7.08	81.40	1.23	7.24	79.70	0.84	7.03	92.14	1.08	6.34	81.89
PC6	0.99	5.81	86.43	1.06	6.24	84.97	1.02	6.02	87.42	1.15	6.77	86.47	0.54	4.53	96.67	0.98	5.77	87.67
PC7	0.88	5.16	91.60	0.95	5.59	90.56	0.92	5.41	92.83	0.87	5.13	91.61	0.32	2.68	99.35	0.86	5.06	92.72
PC8	0.52	3.07	94.67	0.78	4.57	95.12	0.48	2.83	95.67	0.62	3.67	95.27	0.07	0.56	99.90	0.52	3.05	95.77
PC9	0.44	2.61	97.27	0.41	2.40	97.52	0.35	2.06	97.73	0.42	2.50	97.77	0.01	0.06	99.96	0.44	2.56	98.33
PC10	0.34	1.98	99.26	0.27	1.57	99.09	0.28	1.62	99.35	0.28	1.63	99.40	0.00	0.03	99.99	0.21	1.21	99.54
PC11	0.10	0.59	99.84	0.13	0.75	99.84	0.08	0.49	99.83	0.08	0.50	99.90	0.00	0.01	100.00	0.06	0.35	99.89
PC12	0.01	0.08	99.92	0.01	0.07	99.91	0.01	0.07	99.91	0.01	0.04	99.94	0.00	0.00	100.00	0.01	0.06	99.94
PC13	0.01	0.05	99.97	0.01	0.04	99.94	0.01	0.04	99.95	0.01	0.03	99.97				0.00	0.02	99.96
PC14	0.00	0.02	99.98	0.01	0.03	99.98	0.01	0.03	99.98	0.00	0.01	99.98				0.00	0.02	99.98
PC15	0.00	0.01	99.99	0.00	0.01	99.99	0.00	0.02	99.99	0.00	0.01	99.99				0.00	0.01	99.99
PC16	0.00	0.01	100.00	0.00	0.01	100.00	0.00	0.01	100.00	0.00	0.01	100.00				0.00	0.01	100.00
PC17	0.00	0.00	100.00				0.00	0.00	100.00	0.00	0.00	100.00				0.00	0.00	100.00

[†] PHT, FLL, FLW, FLA, FLS were not evaluated in Kinston 2014.

Table 5.5 Principle component analysis of the MD01W233-06-1 \times SS8641 doubled haploid population based on sixteen agronomic traits including grain yield (GYLD), grains per spike (GPS), grain weight per spike (GWPS), spikes per square meter (SPSM), and thousand-grain-weight (TGW), plant height (PHT), flag leaf length (FLL), flag leaf width (FLW), flag leaf area (FLA), flag leaf shape (FLS), spike length (SL), sterile spikelet number per spike (SSN), fertile spikelet number per spike (FSN), total spikelet number per spike (TSN), spike compactness (SC), grain number per spike (GSP), and heading date (HD). Eigenvectors of the first two principle components (PC) are shown.

	Clarksv	ille 2013	Clarksv	ille 2014	Queenst	own 2013	Queenst	own 2014	Kinsto	n 2014 [†]	Ove	erall
	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2
GYLD	-0.197	-0.293	-0.086	-0.042	-0.241	-0.196	-0.045	-0.303	-0.187	-0.152	-0.230	0.227
GPS	0.374	-0.118	0.349	-0.262	0.298	-0.302	0.343	-0.227	0.439	-0.149	0.311	0.255
GWPS	0.315	-0.254	0.302	-0.250	0.215	-0.375	0.302	-0.321	0.250	-0.314	0.230	0.367
SPSM	-0.355	-0.081	-0.312	0.174	-0.332	0.039	-0.286	0.013	-0.356	0.075	-0.338	-0.080
TGW	-0.046	-0.264	0.046	0.095	-0.135	-0.109	-0.079	-0.098	-0.215	-0.172	-0.094	0.114
PHT	0.086	-0.165	-0.013	0.010	-0.003	0.029	0.149	-0.070			0.043	0.138
FLL	0.277	-0.025	0.277	0.148	0.307	0.099	0.317	0.119			0.311	0.029
FLW	0.156	0.177	0.262	0.207	0.246	0.172	0.189	0.378			0.247	-0.233
FLA	0.281	0.075	0.339	0.220	0.335	0.162	0.309	0.293			0.347	-0.119
FLS	0.166	-0.140	0.046	-0.028	0.098	-0.045	0.132	-0.217			0.089	0.212
SL	0.341	-0.060	0.354	-0.012	0.299	-0.183	0.344	-0.063	0.321	-0.163	0.295	0.163
SSN	-0.144	0.291	-0.051	0.449	-0.011	0.413	-0.019	0.273	-0.046	0.423	0.031	-0.346
FSN	0.334	0.191	0.361	0.087	0.363	-0.046	0.375	0.001	0.450	0.101	0.356	-0.016
TSN	0.279	0.322	0.314	0.283	0.336	0.161	0.359	0.125	0.397	0.279	0.349	-0.164
SC	-0.104	0.394	-0.114	0.301	-0.002	0.365	-0.078	0.234	0.070	0.462	0.005	-0.351
GSP	0.192	-0.322	0.158	-0.445	0.137	-0.402	0.154	-0.327	0.218	-0.335	0.112	0.379
HD	0.076	0.433	0.152	0.369	0.221	0.347	0.108	0.439	0.137	0.449	0.196	-0.396

† PHT, FLL, FLW, FLA, FLS were not evaluated in Kinston 2014.

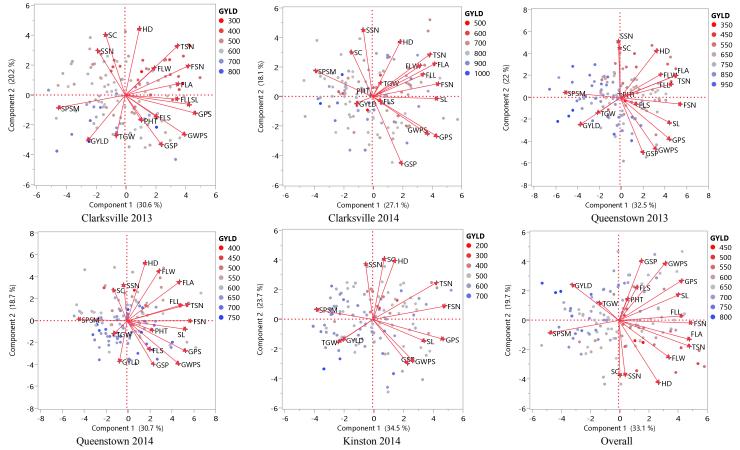
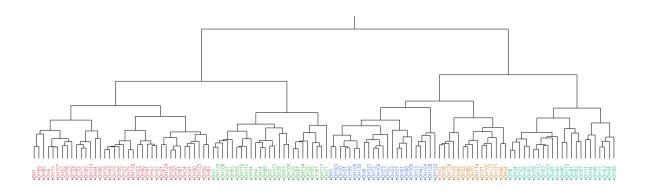


Figure 5.1 Principal component analysis: biplot summarizing the relationship among grain yield components, plant architecture, and spike morphology for the MD01W233-06-1 × SS8641doubled haploid population evaluated in five trials from 2013 to 2014. Traits are grain yield (GYLD), grains per spike (GPS), grain weight per spike (GWPS), spikes per square meter (SPSM), and thousand-grain-weight (TGW), plant height (PHT), flag leaf length (FLL), flag leaf width (FLW), flag leaf area (FLA), flag leaf shape (FLS), spike length (SL), sterile spikelet number per spike (SSN), fertile spikelet number per spike (FSN), total spikelet number per spike (TSN), spikelet compactness (SC), and grain number per spikelet (GSP). PHT, FLL, FLW, FLA, FLS were not evaluated at Kinston 2014.



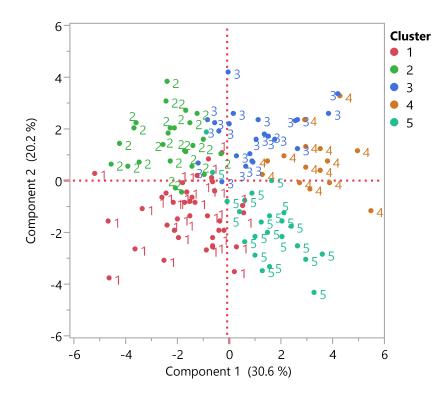


Figure 5.21 Dendrogram of cluster analysis and scatter diagram of the doubled-haploid lines for the first two principal components at Clarksville 2013 (E1).

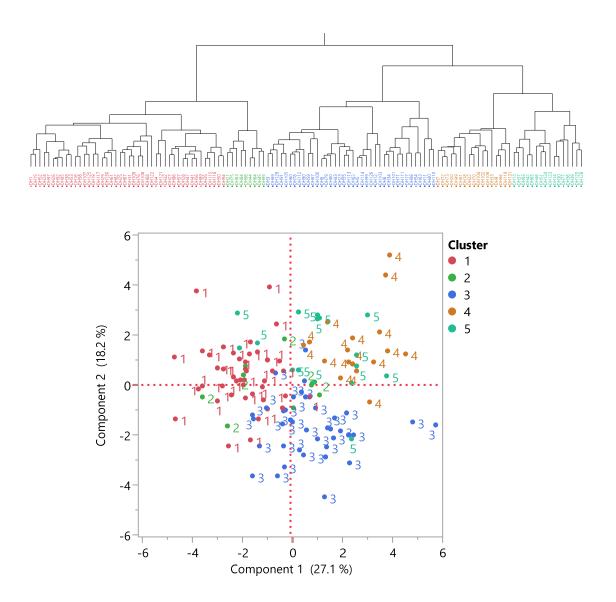


Figure 5.22 Dendrogram of cluster analysis and scatter diagram of the doubled-haploid lines for the first two principal components at Clarksville 2014 (E2).

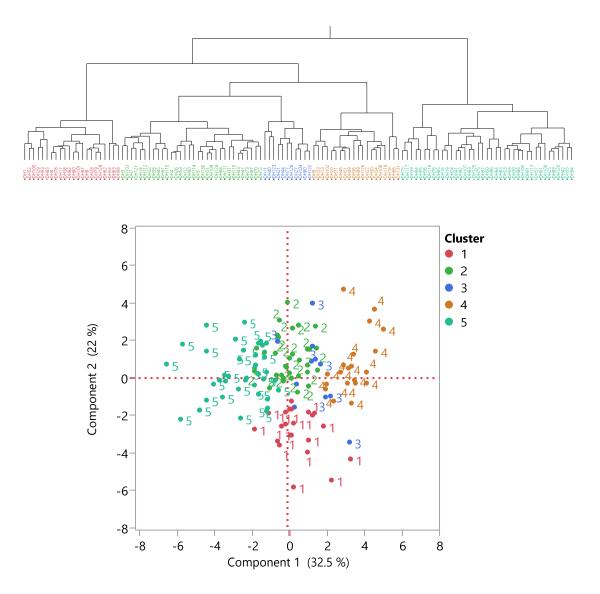


Figure 5.23 Dendrogram of cluster analysis and scatter diagram of the doubled-haploid lines for the first two principal components at Queenstown 2013 (E3).

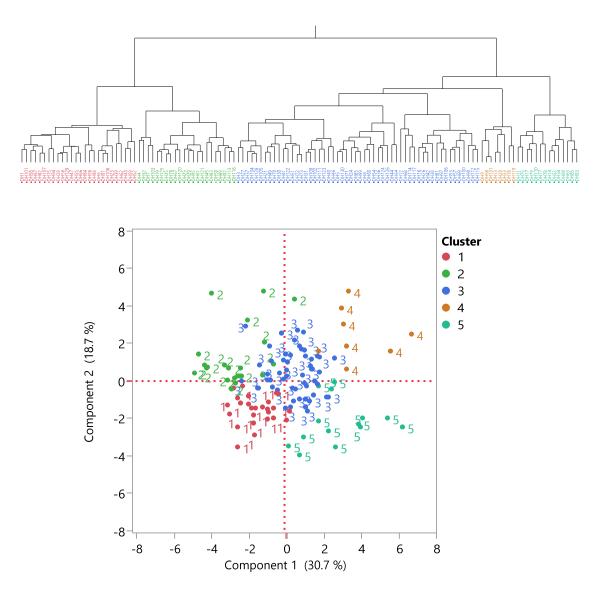


Figure 5.24 Dendrogram of cluster analysis and scatter diagram of the doubled-haploid lines for the first two principal components at Queenstown 2014 (E4).

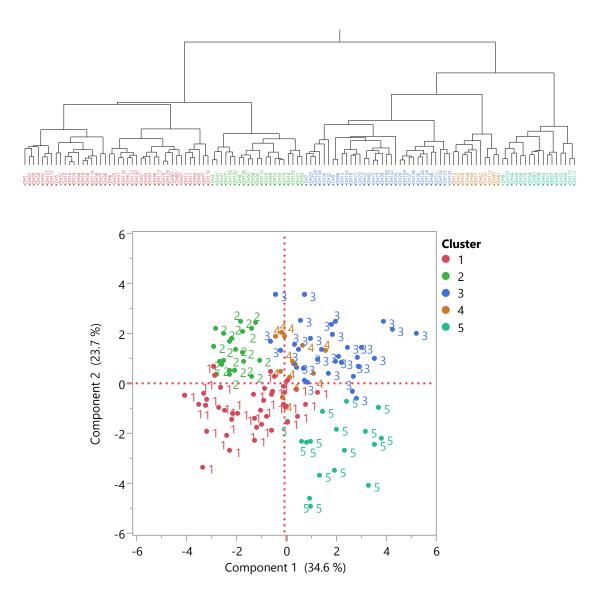


Figure 5.25 Dendrogram of cluster analysis and scatter diagram of the doubled-haploid lines for the first two principal components at Kinston 2014 (E5).

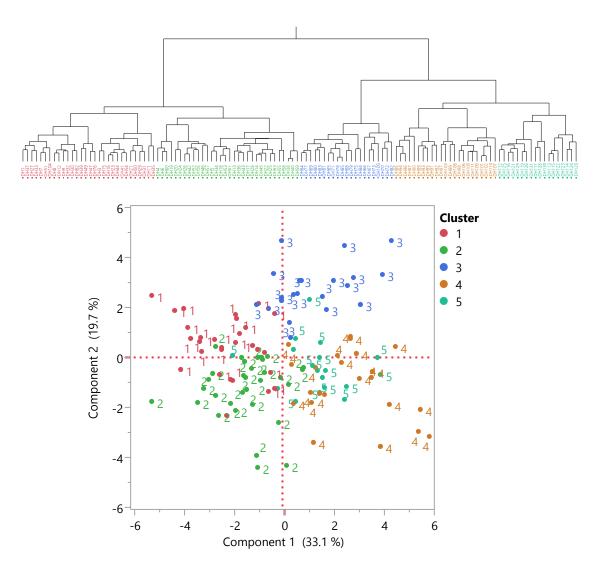


Figure 5.26 Dendrogram of cluster analysis and scatter diagram of the doubled-haploid lines for the first two principal components based on the average of E1, E2, E3, and E4.

Environments	Traits	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5
E1	GYLD	639.64 ± 6.40	561.74 ± 4.83	493.13 ± 6.07	484.99 ± 7.49	578.20 ± 8.01
	GPS	38.15 ± 0.26	35.19 ± 0.20	40.82 ± 0.26	45.10 ± 0.24	43.81 ± 0.30
	GWPS	1.19 ± 0.01	1.08 ± 0.01	1.16 ± 0.01	1.38 ± 0.01	1.37 ± 0.01
	SPSM	540.92 ± 6.65	527.62 ± 5.15	428.18 ± 5.67	359.14 ± 6.16	426.97 ± 5.0
	TGW	32.34 ± 0.18	31.29 ± 0.16	29.19 ± 0.14	31.31 ± 0.14	32.36 ± 0.18
	PHT	87.82 ± 0.41	83.68 ± 0.54	85.28 ± 0.37	87.12 ± 0.45	89.57 ± 0.57
	FLL	13.52 ± 0.09	12.45 ± 0.09	14.51 ± 0.13	14.54 ± 0.10	13.59 ± 0.13
	FLW	1.44 ± 0.01	1.46 ± 0.01	1.53 ± 0.01	1.54 ± 0.01	1.44 ± 0.01
	FLA	15.47 ± 0.17	14.46 ± 0.14	17.55 ± 0.18	17.77 ± 0.13	15.53 ± 0.19
	FLS	9.48 ± 0.06	8.61 ± 0.08	9.61 ± 0.12	9.56 ± 0.08	9.54 ± 0.10
	SL	6.66 ± 0.03	6.67 ± 0.04	7.02 ± 0.03	7.64 ± 0.04	7.41 ± 0.04
	SSN	1.81 ± 0.04	2.18 ± 0.04	1.99 ± 0.03	1.70 ± 0.04	1.40 ± 0.03
	FSN	13.38 ± 0.05	13.96 ± 0.07	14.80 ± 0.08	15.84 ± 0.07	14.90 ± 0.04
	TSN	15.19 ± 0.05	16.14 ± 0.07	16.80 ± 0.08	17.54 ± 0.07	16.30 ± 0.05
	SC	2.29 ± 0.01	2.43 ± 0.01	2.40 ± 0.01	2.31 ± 0.01	2.21 ± 0.01
	GSP	2.85 ± 0.02	2.52 ± 0.01	2.76 ± 0.01	2.85 ± 0.01	2.94 ± 0.02
	HD	132.22 ± 0.13	133.90 ± 0.11	135.11 ± 0.11	134.47 ± 0.06	131.57 ± 0.1
E2	GYLD	789.07 ± 7.10	888.68 ± 5.20	770.68 ± 6.44	756.12 ± 5.43	797.80 ± 9.0
	GPS	32.94 ± 0.18	33.31 ± 0.15	38.17 ± 0.21	38.13 ± 0.22	35.97 ± 0.33
	GWPS	0.91 ± 0.01	1.06 ± 0.01	1.08 ± 0.01	1.05 ± 0.01	0.97 ± 0.01
	SPSM	882.49 ± 8.33	852.99 ± 6.89	722.89 ± 6.07	729.60 ± 6.08	844.23 ± 9.1
	TGW	28.79 ± 0.18	33.14 ± 0.07	29.03 ± 0.16	30.59 ± 0.19	28.30 ± 0.23
	PHT	87.62 ± 0.45	95.30 ± 0.49	88.50 ± 0.60	89.37 ± 0.42	88.67 ± 0.29
	FLL	14.58 ± 0.09	15.38 ± 0.06	15.28 ± 0.12	16.10 ± 0.07	17.21 ± 0.08
	FLW	1.40 ± 0.01	1.42 ± 0.01	1.40 ± 0.01	1.59 ± 0.01	1.39 ± 0.01
	FLA	16.21 ± 0.14	17.35 ± 0.11	17.06 ± 0.21	20.33 ± 0.17	18.97 ± 0.18
	FLS	10.44 ± 0.07	10.89 ± 0.07	10.94 ± 0.09	10.18 ± 0.06	12.47 ± 0.08
	SL	6.95 ± 0.03	7.33 ± 0.04	7.33 ± 0.05	7.56 ± 0.03	7.52 ± 0.05
	SSN	2.23 ± 0.03	2.40 ± 0.03	1.84 ± 0.03	2.48 ± 0.04	2.42 ± 0.03
	FSN	14.68 ± 0.06	14.35 ± 0.08	15.36 ± 0.06	16.14 ± 0.05	15.97 ± 0.08
	TSN	16.91 ± 0.06	16.75 ± 0.07	17.20 ± 0.06	18.62 ± 0.06	18.39 ± 0.07
	SC	2.44 ± 0.01	2.29 ± 0.01	2.36 ± 0.01	2.47 ± 0.01	2.46 ± 0.01
	GSP	2.09 ± 0.01	2.14 ± 0.01	2.34 ± 0.01	2.19 ± 0.01	2.08 ± 0.02
	HD	141.42 ± 0.11	141.50 ± 0.07	140.92 ± 0.12	143.59 ± 0.13	142.00 ± 0.1

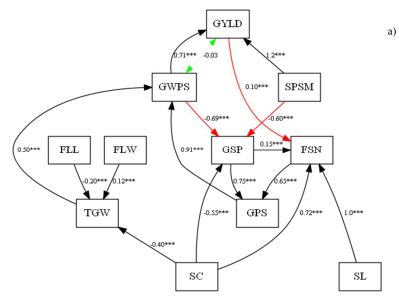
Table 5.6 Mean and standard error for five clusters based on seventeen yield related traits evaluated at Clarksville 2013 (E1), Clarksville 2014 (E2), Queenstown 2013 (E3), Queenstown 2014 (E4), Kinston 2014 (E5), and average of five environments.

Table 5.6 Continued

Environments	Traits	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5
E3	GYLD	804.35 ± 5.83	672.72 ± 8.33	612.83 ± 8.42	659.55 ± 8.19	825.29 ± 9.62
	GPS	49.36 ± 0.27	41.67 ± 0.24	43.34 ± 0.39	47.65 ± 0.30	39.51 ± 0.27
	GWPS	1.61 ± 0.01	1.33 ± 0.01	1.39 ± 0.02	1.51 ± 0.01	1.33 ± 0.01
	SPSM	506.02 ± 4.75	507.85 ± 5.63	446.12 ± 6.34	438.93 ± 4.67	629.89 ± 9.94
	TGW	32.2 ± 0.17	31.32 ± 0.15	31.92 ± 0.20	31.66 ± 0.16	33.22 ± 0.19
	PHT	96.11 ± 0.50	94.86 ± 0.47	104.28 ± 0.41	98.66 ± 0.53	100.31 ± 0.43
	FLL	16.87 ± 0.11	17.11 ± 0.09	19.57 ± 0.12	18.96 ± 0.09	16.22 ± 0.10
	FLW	1.64 ± 0.01	1.71 ± 0.01	1.59 ± 0.01	1.87 ± 0.01	1.62 ± 0.01
	FLA	21.89 ± 0.20	23.21 ± 0.18	24.73 ± 0.26	28.08 ± 0.21	20.78 ± 0.18
	FLS	10.37 ± 0.07	10.06 ± 0.06	12.41 ± 0.07	10.22 ± 0.08	10.09 ± 0.07
	SL	7.48 ± 0.04	7.20 ± 0.03	7.35 ± 0.04	7.69 ± 0.03	6.70 ± 0.03
	SSN	1.11 ± 0.04	1.92 ± 0.04	1.62 ± 0.05	1.84 ± 0.05	1.75 ± 0.04
	FSN	15.26 ± 0.05	14.88 ± 0.05	14.99 ± 0.06	16.26 ± 0.05	13.96 ± 0.07
	TSN	16.38 ± 0.06	16.80 ± 0.06	16.61 ± 0.04	18.09 ± 0.07	15.71 ± 0.08
	SC	2.20 ± 0.01	2.34 ± 0.01	2.27 ± 0.01	2.36 ± 0.01	2.36 ± 0.01
	GSP	3.13 ± 0.01	2.66 ± 0.01	2.76 ± 0.02	2.79 ± 0.02	2.66 ± 0.02
	HD	124.84 ± 0.21	128.91 ± 0.18	129.41 ± 0.17	130.5 ± 0.21	125.96 ± 0.22
E4	GYLD	657.02 ± 3.15	601.17 ± 3.10	595.94 ± 6.01	553.28 ± 2.13	655.64 ± 4.44
	GPS	39.42 ± 0.20	34.50 ± 0.21	39.97 ± 0.24	42.94 ± 0.28	44.83 ± 0.36
	GWPS	1.12 ± 0.01	1.00 ± 0.01	1.11 ± 0.01	1.20 ± 0.01	1.32 ± 0.01
	SPSM	591.24 ± 5.10	603.86 ± 2.58	539.76 ± 4.95	465.42 ± 3.43	500.91 ± 4.10
	TGW	28.97 ± 0.16	30.14 ± 0.20	28.57 ± 0.15	29.02 ± 0.21	30.16 ± 0.17
	PHT	76.85 ± 0.34	73.53 ± 0.36	75.55 ± 0.52	78.16 ± 0.34	79.49 ± 0.49
	FLL	13.99 ± 0.08	13.93 ± 0.08	15.25 ± 0.10	16.66 ± 0.09	15.59 ± 0.08
	FLW	1.32 ± 0.00	1.41 ± 0.01	1.44 ± 0.01	1.61 ± 0.01	1.36 ± 0.01
	FLA	14.60 ± 0.09	15.65 ± 0.17	17.47 ± 0.15	21.39 ± 0.22	16.86 ± 0.13
	FLS	10.67 ± 0.07	9.92 ± 0.06	10.64 ± 0.09	10.35 ± 0.05	11.55 ± 0.09
	SL	6.47 ± 0.03	6.38 ± 0.03	6.84 ± 0.04	7.19 ± 0.03	7.47 ± 0.04
	SSN	1.02 ± 0.03	1.51 ± 0.04	1.14 ± 0.03	1.51 ± 0.04	1.13 ± 0.03
	FSN	13.58 ± 0.05	13.09 ± 0.05	14.15 ± 0.05	15.21 ± 0.05	15.07 ± 0.07
	TSN	14.61 ± 0.06	14.60 ± 0.06	15.29 ± 0.06	16.72 ± 0.04	16.20 ± 0.06
	SC	2.26 ± 0.01	2.30 ± 0.01	2.25 ± 0.01	2.33 ± 0.01	2.18 ± 0.01
	GSP	2.90 ± 0.01	2.62 ± 0.01	2.81 ± 0.02	2.81 ± 0.01	2.96 ± 0.02
	HD	138.46 ± 0.10	140.07 ± 0.13	140.30 ± 0.12	142.25 ± 0.09	138.54 ± 0.12

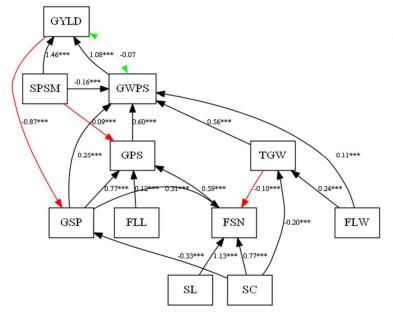
Table 5.6 Continued

Environment	Traits	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5
E5	GYLD	591.65 ± 5.44	585.89 ± 5.01	545.90 ± 4.71	400.65 ± 6.28	544.87 ± 5.99
	GPS	40.11 ± 0.22	37.55 ± 0.15	45.84 ± 0.35	40.47 ± 0.20	48.73 ± 0.19
	GWPS	1.17 ± 0.01	1.10 ± 0.01	1.20 ± 0.01	1.03 ± 0.01	1.35 ± 0.01
	SPSM	508.88 ± 5.51	534.13 ± 3.68	458.08 ± 4.65	388.77 ± 5.29	404.32 ± 3.96
	TGW	28.91 ± 0.23	29.26 ± 0.20	25.74 ± 0.14	24.52 ± 0.26	27.27 ± 0.21
	SL	7.46 ± 0.04	7.07 ± 0.03	7.76 ± 0.04	7.42 ± 0.03	8.05 ± 0.05
	SSN	2.21 ± 0.04	2.96 ± 0.04	2.74 ± 0.04	2.30 ± 0.04	1.82 ± 0.03
	FSN	15.40 ± 0.08	15.09 ± 0.05	17.25 ± 0.08	16.15 ± 0.05	16.70 ± 0.08
	TSN	17.61 ± 0.09	18.05 ± 0.05	19.99 ± 0.08	18.45 ± 0.05	18.52 ± 0.09
	SC	2.37 ± 0.01	2.56 ± 0.01	2.59 ± 0.01	2.50 ± 0.01	2.31 ± 0.01
	GSP	2.60 ± 0.01	2.48 ± 0.01	2.65 ± 0.01	2.51 ± 0.02	2.92 ± 0.01
	HD	113.25 ± 0.23	116.81 ± 0.12	119.03 ± 0.22	114.95 ± 0.17	112.26 ± 0.32
All five trials	GYLD	692.85 ± 5.00	654.56 ± 4.01	677.91 ± 3.08	589.85 ± 5.71	627.68 ± 5.26
	GPS	38.68 ± 0.18	37.06 ± 0.19	44.33 ± 0.23	42.53 ± 0.27	40.68 ± 0.30
	GWPS	1.15 ± 0.00	1.1 ± 0.01	1.34 ± 0.01	1.22 ± 0.01	1.18 ± 0.01
	SPSM	617.91 ± 5.00	612.58 ± 4.18	519.57 ± 3.94	497.52 ± 4.10	547.24 ± 3.53
	TGW	30.1 ± 0.18	29.9 ± 0.15	30.56 ± 0.19	29.43 ± 0.14	29.56 ± 0.23
	PHT	88.28 ± 0.30	84.37 ± 0.43	89.45 ± 0.46	85.89 ± 0.48	91.36 ± 0.31
	FLL	14.65 ± 0.08	14.66 ± 0.07	15.73 ± 0.07	15.8 ± 0.11	16.39 ± 0.10
	FLW	1.44 ± 0.01	1.49 ± 0.01	1.47 ± 0.01	1.64 ± 0.01	1.46 ± 0.01
	FLA	16.86 ± 0.14	17.43 ± 0.11	18.44 ± 0.12	20.72 ± 0.22	19.12 ± 0.17
	FLS	10.22 ± 0.06	9.89 ± 0.06	10.77 ± 0.06	9.7 ± 0.06	11.31 ± 0.08
	SL	6.67 ± 0.03	7.03 ± 0.03	7.52 ± 0.03	7.44 ± 0.03	7.36 ± 0.04
	SSN	1.73 ± 0.03	2.04 ± 0.03	1.51 ± 0.02	1.93 ± 0.04	2.11 ± 0.03
	FSN	14.09 ± 0.04	14.52 ± 0.05	15.31 ± 0.06	15.8 ± 0.06	15.41 ± 0.07
	TSN	15.82 ± 0.05	16.56 ± 0.05	16.81 ± 0.05	17.73 ± 0.07	17.51 ± 0.06
	SC	2.38 ± 0.01	2.36 ± 0.01	2.24 ± 0.01	2.39 ± 0.01	2.39 ± 0.01
	GSP	2.69 ± 0.01	2.49 ± 0.01	2.84 ± 0.01	2.63 ± 0.01	2.57 ± 0.01
	HD	130.29 ± 0.14	131.92 ± 0.16	129.42 ± 0.12	133.44 ± 0.16	132.94 ± 0.12



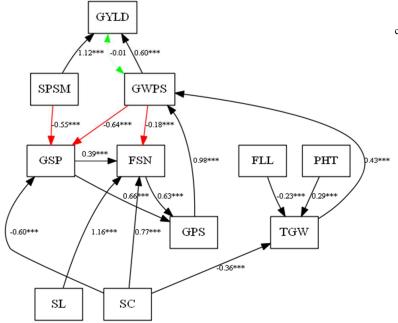
) Phenotype network at 2013 Clarksville, MD (E1).

> Model fit indices: SRMR=0.04 RMSEA=0.06 NNFI=0.97 CFI=0.98



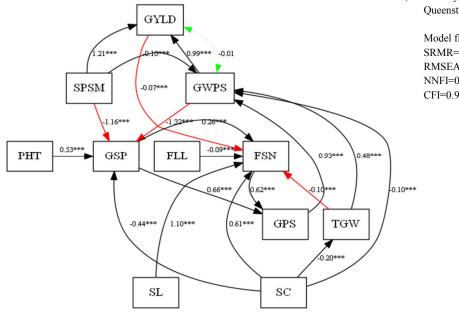
b) Phenotype network at 2014 Clarksville, MD (E2).

> Model fit indices: SRMR=0.03 RMSEA=0.05 NNFI=0.98 CFI=0.99



c) Phenotype network at 2013 Queenstwon, MD (E3).

> Model fit indices: SRMR=0.03 RMSEA=0.06 NNFI=0.97 CFI=0.98



d) Phenotype network at 2014 Queenstwon, MD (E4).

> Model fit indices: SRMR=0.03 RMSEA=0.07 NNFI=0.96 CFI=0.98

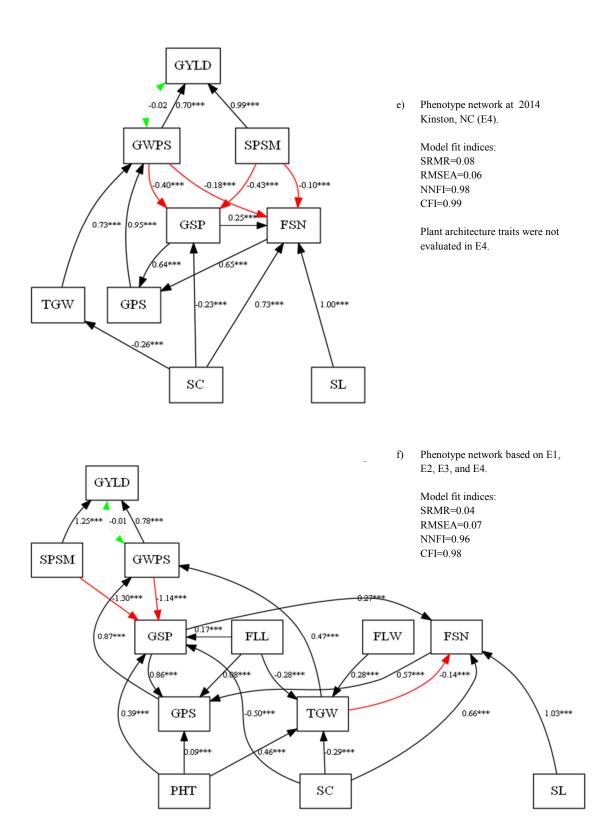


Figure 5.3 Graphical representation of the structural equation modeling for the phenotypic network based on data from a) Clarksville 2013, b) Clarksville 2014, c) Queenstown 2013, d) Queenstown 2014, f) Kinston 2014, and g) First four environments averaged. Red arrows indicate negative contribution. Green arrows indicate error covariance.

Appendix A.

SSR Marker	Source	Reference
Xbarc100	USDA-ARS Beltsville Agricultural Research Center	(Song et al., 2005) Theor Appl Genet 110: 550–560
Xbarc101	USDA-ARS Beltsville Agricultural Research Center	(Song et al., 2005) Theor Appl Genet 110: 550–560
Xbarc10	USDA-ARS Beltsville Agricultural Research Center	(Song et al., 2005) Theor Appl Genet 110: 550–560
Xbarc127	USDA-ARS Beltsville Agricultural Research Center	(Song et al., 2005) Theor Appl Genet 110: 550–560
Xbarc12	USDA-ARS Beltsville Agricultural Research Center	(Song et al., 2005) Theor Appl Genet 110: 550–560
Xbarc147	USDA-ARS Beltsville Agricultural Research Center	(Song et al., 2005) Theor Appl Genet 110: 550–560
Xbarc163	USDA-ARS Beltsville Agricultural Research Center	(Song et al., 2005) Theor Appl Genet 110: 550–560
Xbarc164	USDA-ARS Beltsville Agricultural Research Center	(Song et al., 2005) Theor Appl Genet 110: 550–560
Xbarc170	USDA-ARS Beltsville Agricultural Research Center	(Song et al., 2005) Theor Appl Genet 110: 550–560
Xbarc28	USDA-ARS Beltsville Agricultural Research Center	(Song et al., 2005) Theor Appl Genet 110: 550–560
Xbarc45	USDA-ARS Beltsville Agricultural Research Center	(Song et al., 2005) Theor Appl Genet 110: 550–560
Xbarc59	USDA-ARS Beltsville Agricultural Research Center	(Song et al., 2005) Theor Appl Genet 110: 550–560
Xbarc80	USDA-ARS Beltsville Agricultural Research Center	(Song et al., 2005) Theor Appl Genet 110: 550–560
Xgdm136	Gatersleben D-genome Microsatellite	(Pestsova et al.,2000) Genome 43: 689-697
Xgwm111	Gatersleben wheat microsatellite	(Roder et al., 1998) Genetics 149: 2007-2024
Xgwm11	Gatersleben wheat microsatellite	(Roder et al., 1998) Genetics 149: 2007-2025
Xgwm261	Gatersleben wheat microsatellite	(Roder et al., 1998) Genetics 149: 2007-2026
Xgwm282	Gatersleben wheat microsatellite	(Roder et al., 1998) Genetics 149: 2007-2027
Xgwm304	Gatersleben wheat microsatellite	(Roder et al., 1998) Genetics 149: 2007-2028
Xgwm319	Gatersleben wheat microsatellite	(Roder et al., 1998) Genetics 149: 2007-2029
Xwmc273	Wheat Microsatellite Consortium	Somers and Isaac, 2004. SSRs from the Wheat Microsatellite Consortium
Xwmc496	Wheat Microsatellite Consortium	http://wheat.pw.usda.gov/ggpages/SSR/WMC/

Table A.1 Source of simple sequence repeats (SSRs) on the linkage map constructed in this study

Appendix B.

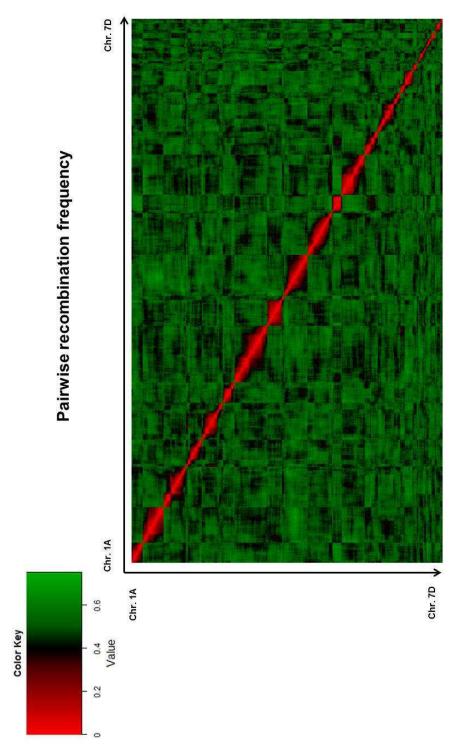


Figure B.1 Heat map of the genetic linkage map based on recombination frequencies among 859 DNA markers. Markers are aligned along each chromosome from 1A to 7D.

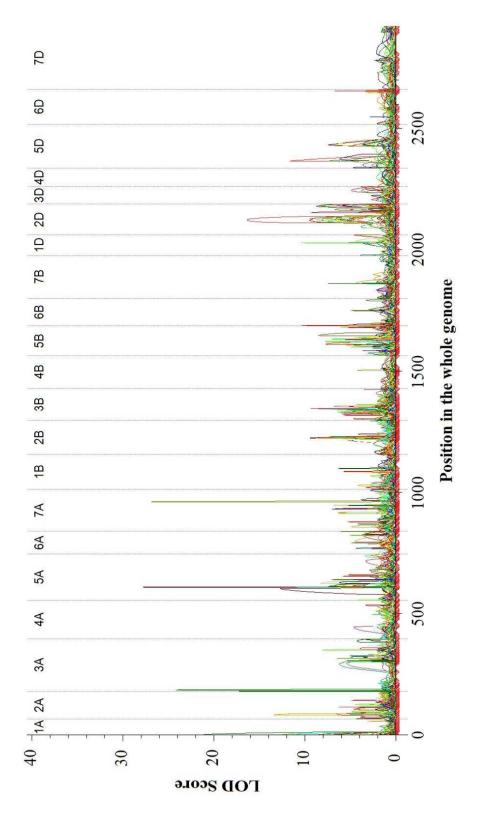


Figure B.2 Genome-wide distribution of LOD score. Markers are aligned along each chromosome from 1A to 7D according to their order on each chromosome. Unit of X-axis: cM.

Appendix C.

QTL	Trait	Marker interval	LOD	PVE	Additive effect		
QFlw.cz-2A.2	FLW	Xsnp2471-Xsnp2461	13.3	31.2%	0.13	Major	
QFsn.cz-1A	FSN	Xsnp1970-Xbarc28	20.6	30.0%	0.65	Major	*
QGps.cz-1A.1	GPS	Xsnp1970-Xbarc28	14.2	26.5%	2.44	Major	
QGps.cz-1A.2	GPS	Xbarc28-Xsnp2005	21.2	44.1%	2.95	Major	*
QGps.cz-3A.2	GPS	Xsnp3049-Xsnp3021	24.1	52.0%	-3.20	Major	
QGws.cz-1A.1	GWPS	Xwmc496-Xsnp1970	12.2	28.6%	0.08	Major	
QGws.cz-1A.2	GWPS	Xsnp1970-Xbarc28	11.5	33.2%	0.06	Major	*
QPht.cz-5B.1	PHT	Xsnp4068-Xsnp4012	9.3	20.1%	2.86	Major	
QSc.cz-5A.3	SC	Xgwm304-Xsnp996	27.7	80.2%	-0.15	Major	*
QSc.cz-2B.1	SC	Xsnp2773-Xgwm319	9.3	21.6%	0.07	Major	*
QSc.cz-5A.1	SC	Xsnp279-Xsnp3878	12.7	26.7%	0.09	Major	
QSl.cz-1A	SL	Xsnp1970-Xbarc28	9.3	22.4%	0.25	Major	*
QSsm.cz-1A.1	SPSM	Xwmc496-Xsnp1970	13.9	30.1%	-50.85	Major	*
QSsm.cz-1A.2	SPSM	Xsnp1970-Xbarc28	15.6	22.1%	-34.04	Major	
QSsm.cz-1A.3	SPSM	Xbarc28-Xsnp2005	8.3	23.0%	-51.60	Major	*
QSsn.cz-2D.1	SSN	Xsnp2862-XPpdD1	16.3	30.0%	-0.31	Major	
QTgw.cz-7A.5	TGW	Xsnp4588-Xsnp4620	26.8	71.2%	-1.77	Major	
QTsn.cz-1A	TSN	Xsnp1970-Xbarc28	13.2	20.0%	0.57	Major	
QTsn.cz-2D.3	TSN	XPpdD1-Xsnp2869	6.5	20.9%	-0.41	Major	
QFla.cz-1A.1	FLA	Xsnp1970-Xbarc28	8.3	16.8%	1.36	New	
QFla.cz-1A.2	FLA	Xbarc28-Xsnp2005	4.3	9.1%	0.70	New	
QFla.cz-1B	FLA	Xsnp4503-Xsnp2181	4.1	9.4%	0.71	New	
QFla.cz-2A.1	FLA	Xsnp2471-Xsnp2461	13.1	28.7%	4.18	New	
QFla.cz-2A.2	FLA	Xsnp2461-Xsnp2466	6.5	13.4%	1.23	New	
QFla.cz-2D.1	FLA	Xsnp2862-XPpdD1	9.5	20.9%	-1.53	New	
QFla.cz-2D.2	FLA	XPpdD1-Xsnp2869	8.7	24.1%	-1.10	New	*
QFla.cz-2D.3	FLA	Xsnp2804-Xsnp1766	4.6	9.6%	-0.72	New	
QFla.cz-3B	FLA	Xsnp3407-Xbarc147	3.8	6.8%	2.03	New	
QFla.cz-5B.1	FLA	Xsnp4140-Xsnp4114	3.3	7.9%	-0.63	New	
QFla.cz-5B.2	FLA	Xsnp4083-Xsnp3988	3.2	11.4%	-2.47	New	
QFla.cz-6A	FLA	Xsnp473-Xsnp4228	3.2	10.1%	-0.76	New	
QFll.cz-1A.1	FLL	Xsnp1970-Xbarc28	4.5	10.0%	0.76	New	*
QFll.cz-2D	FLL	XPpdD1-Xsnp2869	7.5	20.6%	-0.58	New	*
QGws.cz-5B	GWPS	Xsnp4130-Xsnp3884	3.6	7.3%	-0.04	New	
QGws.cz-7B	GWPS	Xsnp4927-Xsnp489	3.1	7.5%	0.03	New	
Qyld.cz-2A	GYLD	Xsnp2477-Xsnp2432	4.3	9.9%	25.21	New	
QYld.cz-5B.2	GYLD	Xsnp4011-Xsnp4073	4.5	10.3%	25.67	New	
QPht.cz-2D.2	PHT	Xsnp2795-Xsnp708	8.4	22.0%	2.79	New	
QSl.cz-5A.1	SL	Xsnp3819-Xsnp3789	8.2	13.0%	0.20	New	
QSl.cz-5A.2	SL	Xsnp3789-Xsnp3844	6.2	12.5%	0.18	New	
QSl.cz-5A.3	SL	Xsnp3812-Xsnp3856	4.0	9.7%	0.16	New	
QSl.cz-5A.4	SL	Xsnp3852-Xsnp3843	7.0	13.1%	0.19	New	
QSl.cz-5A.5	SL	Xsnp3849-Xsnp3841	2.8	6.7%	0.13	New	
QTgw.cz-3A.6	TGW	Xsnp2951-Xsnp2971	4.2	6.7%	-0.57	New	

Table C.1 Summary of major and possible new QTLs identified in the present study. QTLs detected in multiple environments were indicated by asterisk.

Appendix D.

	e of five envir						~
No.	Name	E1	E2	E4	E4	E5	five average
1	DH1	1	1	1	1	1	1
2	DH3	2	3	2	3	2	1
3	DH4	2	1	2	2	2	2
4	DH5	3	3	2	3	1	2
5	DH6	1	3	1	1	1	3
6	DH7	2	4	2	2	3	2
7	DH8	5	3	1	3	5	3
8	DH9	3	4	4	4	3	4
9	DH11	5	3	3	5	1	3
10	DH12	4	3	2	3	4	4
11	DH12 DH13	3	5	4	4	3	5
12	DH15 DH14	2	5	2	5	2	5
13	DH15	1	1	5	1	1	1
13	DH15 DH16	1	1	5	3	1	1
				1		1	
15	DH17	5	3		5		3
16	DH18	4	4	4	4	3	4
17	DH19	1	1	5	2	1	1
18	DH20	3	4	4	4	3	4
19	DH21	1	2	3	3	2	5
20	DH22	4	4	4	5	3	4
21	DH23	1	3	5	1	5	1
22	DH24	1	1	5	3	1	1
23	DH25	5	1	5	2	1	2
24	DH26	2	1	2	3	4	2
25	DH27	1	1	3	3	2	-
26	DH27 DH28	1	1	1	1	2	1
20 27	DH28 DH29	2	1	1	2	3	2
28	DH29 DH30	1	5	4	3	4	5
29	DH31	3	1	2	3	1	2
30	DH32	3	1	2	2	3	2
31	DH33	3	4	4	4	3	4
32	DH34	5	3	4	5	5	3
33	DH35	2	1	2	2	2	2
34	DH36	4	5	4	3	3	4
35	DH37	3	5	2	3	3	5
36	DH38	5	1	1	3	4	3
37	DH39	2	5	5	1	3	1
38	DH40	5	3	3	3	4	5
39	DH41	1	1	5	3	2	2
40	DH42	3	5	5	3	3	5
41	DH42 DH43	1	3	2	1	4	1
42	DH45 DH44	5	2	3	3	5	5
42 43	DH44 DH45	1	2	2	2	1	2
43 44		4					
	DH46		5	4	3	3	4
45	DH47	1	1	2	1	2	2
46	DH49	5	4	4	3	5	4
47	DH50	1	1	5	2	2	2
48	DH51	3	5	4	3	3	5
49	DH52	1	1	1	1	1	1
50	DH53	2	1	2	3	2	2
51	DH54	4	3	1	3	5	3
52	DH55	2	3	5	1	2	1
53	DH56	2	1	5	1	1	1
54	DH57	2	1	5	3	4	1
55	DH58	1	1	5	1	1	1
56	DH58 DH59	1	3	5	1	1	1
50 57	DH60	1	3	1	3	5	3
58	DH60 DH61	1 2	3 1	1 2	3 2	5	3 2
59	DH62	1	3	1	1	4	1
60	DH63	5	3	1	5	5	3
61	DH64 DH65	5 5	2 5	5	3 5	1	3
62		5	5	1	5	5	3

Table D.1 Cluster membership of 124 doubled haploid lines based on data from: Clarksville 2013 (E1), Clarksville 2014 (E2), Queenstown 2013 (E3), Queenstown 2014 (E4), Kinston 2014 (E5), and average of five environments.

Table D.1 Continued.

No.	Name	E1	E2	E4	E4	E5	five average
63	DH66	4	4	4	4	3	4
64	DH67	2	1	2	2	1	2
65	DH68	3	1	2	3	4	4
66	DH69	1	3	5	3	5	1
67	DH70	4	4	2	3	3	5
68	DH71	4	3	4	3	3	4
69	DH72	3	4	2	3	3	4
70	DH73	3	4	2	3	3	4
71	DH75	1	2	5	5	1	1
72	DH76	1	1	5	2	2	2
73	DH77	2	5	3	5	1	5
74	DH78	5	3	1	5	5	3
75	DH79	1	3	1	5	1	3
76	DH80	4	3	3	5	1	3
77	DH81	5	4	5	3	4	4
78	DH82	5	1	1	1	1	1
79	DH83	1	2	5	2	2	5
80	DH84	1	2	5	1	1	1
81	DH85	1	1	5	3	1	2
82	DH86	5	1	5	1	1	1
83	DH87	5	3	1	1	5	3
84	DH89	2	1	5	2	2	2
85	DH90	1	3	2	3	1	2
86	DH91	1	3	5	1	1	1
87	DH92	1	1	5	2	1	2
88	DH93	5	5	1	5	5	3
89	DH94	2	1	5	1	2	2
90	DH95	1	2	5	2	1	1
91	DH96	1	2	5	1	1	1
92	DH97	5	1	5	3	1	3
93	DH98	5	3	1	1	5	3
94	DH99	3	3	4	3	3	4
95	DH100	2	3	1	3	3	4
96	DH101	5	3	1	1	5	3
97	DH102	4	4	4	3	3	5
98	DH103	3	3	2	2	3	4
99	DH104	3	4	3	3	3	5
100	DH105	3	3	5	3	2	1
101	DH106	3	4	4	3	3	4
102	DH107	1	1	5	1	1	1
103	DH108	2	1	5	1	2	2
104	DH109	3	1	2	3	3	2
105	DH110	5	3	2	5	5	5
106	DH111	4	3	2	3	5	3
107	DH112	5	3	2	3	4	4
108	DH113	1	3	5	2	1	1
109	DH114	2	3	2	3	1	2
110	DH115	2	1	2	3	2	2 2
111	DH116	2	1	5	2	1	2
112	DH117	2	1	5	3	1	2
113	DH119	4	4	4	4	1	4
114	DH120	2	5	5	2	2	2
115	DH121	2	1	2	2	3	2 2 5
116	DH122	4	1	3	3	3	5
117	DH123	3	5	3	3	1	5
118	DH124	1	5	2	3	3	2
119	DH125	1	1	5	2	2	1
120	DH126	4	3	4	3	3	4
121	DH128	3	5	3	3	3	5
122	DH129	1	3	1	1	1	3
123	DH130	3	1	2	3	1	2 4
124	DH131	3	4	4	4	3	4

Appendix E.

Table E.1 Phenotypic data for yield contributing traits evaluated at Clarksville 2013 (E1), Clarksville 2014 (E2), Queenstown 2013 (E3), Queenstown 2014 (E4), and Kinston 2014 (E5). Two replications at each environment. Missing data is indicated by dot.

No.	Env.	Rep.	Name	GYLD	GPS	GWPS	SPSM	TGW	PHT	FLL	FLW	FLA	FLS	SL	SSN	FSN	TSN	SC	GSP	HD
1	E1	1	DH1	658.7	34.7	1.0	646.4	29.6	86.5	10.9	1.2	10.2	9.3	6.2	1.5	13.3	14.8	2.4	2.6	131
2	E1	1	DH3	696.5	35.3	1.1	636.7	32.7	91.2	15.5	1.6	19.7	9.6	6.1	2.0	12.8		2.4	2.8	134
3	E1	1	DH4	494.4	31.9	1.0	477.2	33.5		12.9	1.6	16.0	8.3	6.5	2.2		16.5		2.2	136
4	E1	1	DH5	499.8	35.1	1.0	483.8	30.3	74.5	15.6	1.6	20.3	9.6	6.9	2.1		15.6		2.6	136
5	E1	1	DH6	697.4	40.4	1.3	543.6	32.7		13.7	1.4	15.2	9.7	6.8	1.3		15.5		2.8	129
6 7	E1 E1	1 1	DH7 DH8	564.1 640.2	32.5	1.0 1.2	560.1 520.5	29.9 30.5	81.2 93.9	13.4	1.5 1.5	16.1 17.1	8.9 9.5	6.3 7.3	2.9 2.2		16.8 16.6	2.7	2.3 2.9	135 132
8	E1	1	DH9	354.9	42.5 39.4	1.2	335.4	29.9	93.9 79.6		1.5	20.4	9.5 9.9	7.2	2.2		18.1		2.9	132
9	E1	1		720.7		1.5		35.1	110.9		1.4		11.2		1.7		16.7		3.0	131
10	E1	1		416.1	41.3	1.2	341.6	30.7		13.0	1.4	15.0	9.0	7.1	1.8		16.4		2.8	132
11	E1	1		482.5	42.5	1.2	389.5	28.0	88.5		1.4		10.6	7.1	2.0		17.8		2.7	137
12	E1	1	DH14	632.4	38.7	1.3	503.1	32.7	87.0	12.6	1.6	15.9	8.1	6.7	2.0	14.7	16.7	2.5	2.6	137
13	E1	1	DH15	640.0	35.3	1.1	579.1	31.8	80.7	12.9	1.4	14.1	9.3	6.6	1.5	13.3	14.8	2.2	2.7	130
14	E1	1		601.1	39.7	1.2	513.8	31.6		13.2	1.5	16.0	8.6	6.4	1.8		15.3		2.9	133
15	E1	1		596.6	40.7	1.4	417.2	34.7	87.4	15.2	1.4	16.4	11.3	7.5	1.3		15.3		2.9	130
16	E1	1		424.7		1.4	307.7	31.0			1.7	18.7	8.0	7.4	1.7		17.8		2.7	135
17	E1	1		660.7	35.3	1.2	573.5	33.4		13.5	1.5	16.2	9.0	6.2	1.9		14.3		2.8	133
18 19	E1 E1	1 1		500.7 583.2	47.7 37.1	1.3 1.2	371.2 488.4	28.8 33.1	73.8 93.7	13.7 15.2	1.6 1.5	17.2 18.1	8.7 10.3	6.7 6.9	1.3 2.8		16.3 16.2		3.2 2.8	134 134
20	E1	1			39.5	1.2		33.4		13.2	1.5	18.4	9.2	7.1	2.8		18.2		2.8 2.5	134
20	E1	1			41.2	1.2	522.5	31.1		16.1	1.4			6.3	1.2	13.2		2.3	3.1	131
22	E1	1			33.4	1.0	744.3	31.0	93.6		1.5	14.6	7.9	6.0	1.8		14.2		2.7	132
23	E1	1		672.5	44.1	1.3	515.4	33.8		13.7	1.4	15.4	9.6	7.4	1.9		16.7		3.0	130
24	E1	1	DH26	644.8	33.1	1.1	609.4	33.1	79.5	12.7	1.5	15.4	8.4	6.6	2.4	13.7	16.1	2.4	2.4	132
25	E1	1	DH27	586.9	41.1	1.2	479.5	30.5	91.3	15.0	1.4	16.9	10.5	6.3	1.4	12.9	14.3	2.3	3.2	134
26	E1	1		602.4	38.7	1.2	514.8	32.0	93.5	13.2	1.5	15.9	8.8	6.4	2.2	14.1	16.3	2.6	2.7	133
27	E1	1		442.6	30.9	1.0	428.0	33.7		12.1	1.4	13.3	8.9	6.9	1.8		15.4		2.3	135
28	E1	1		601.2		1.2	520.9	32.8		15.1	1.6	19.1	9.4	6.5	2.4		15.7		2.6	133
29	E1	1		488.3	36.8	1.0	487.3	29.0	83.2	14.5	1.5	17.1	9.7	6.9	2.0		15.7		2.7	136
30 31	E1 E1	1 1		421.5 415.1	38.4 48.6	1.0 1.0	435.5 400.7	25.7 28.9	81.1 90.0	13.9	1.6 1.7	17.7 21.6	8.6 9.4	7.4 7.1	1.2 2.0		17.6 18.3		2.3 3.0	137 137
31	E1 E1	1		574.3	48.0	1.0	400.7	28.9 30.7	90.0 92.2	15.2	1.7	17.7	9.4 10.3	7.1	1.2		16.4		3.0 3.0	137
33	E1	1		576.1	37.9	1.2	480.1	33.7		11.4	1.9	17.0	6.1	7.1	1.2		15.5		2.8	132
34	E1	1		418.7	40.8	1.3	330.5	31.5		14.7	1.5	17.3	10.1	8.1	1.4		18.4		2.4	135
35	E1	1	DH37	553.4	42.1	1.1	504.0	29.7	92.2	15.6	1.6	19.4	10.1	7.1	2.4		16.8		2.9	134
36	E1	1	DH38	533.9	41.7	1.2	445.7	29.4	82.3	13.8	1.4	15.3	9.8	7.1	1.2	14.4	15.6	2.2	2.9	129
37	E1	1	DH39	576.6	39.7	1.2	499.6	30.1	89.7	10.4	1.1	9.4	9.2	6.1	2.1	15.4	17.5	2.9	2.6	137
38	E1	1		547.8	37.1	1.2	450.5	32.8		12.1	1.4	13.4	9.1	7.7	1.1	14.7		2.1	2.5	132
39	E1	1		601.8		1.1	544.1	30.3	86.3		1.4		12.0		1.3		14.8		2.9	130
40	E1	1		571.0	44.6	1.4	417.1	30.7		16.5	1.4		11.9	7.5	1.5		18.3		2.7	134
41 42	E1 E1	1		615.0	34.9 34.8	1.0	608.3 612.2	31.9	89.7		1.5	16.6	9.0	6.1	2.3		14.6		2.8	134
42	E1 E1	1 1		765.9 641.7		1.3 1.3	505.7	36.0 35.3	106.0 90.6		1.6 1.5	20.7 13.5	9.8 7.7	7.6 7.1	1.9 1.9		15.8 15.8		2.5 2.6	136 133
44	E1	1		478.0	41.8	1.1	416.4	29.4	87.4	15.8	1.6		10.2	7.8	2.3		16.5		2.0	134
45	E1	1		699.0	37.0	1.1	618.6	32.3	86.7	13.8	1.4	15.8	9.6	6.8	2.1		15.6		2.7	135
46	E1	1		599.8	46.2	1.4	435.6	30.9	88.7	14.4	1.5	17.4	9.4	7.6	1.8		16.4		3.2	134
47	E1	1	DH50	669.3	34.4	1.1	585.6	34.4	88.7	15.1	1.6	19.5	9.3	6.2	2.1	12.5	14.6	2.3	2.8	131
48	E1	1	DH51	507.0	42.6	1.0		29.2			1.6	21.5	10.0	7.2	2.6	15.1	17.7	2.5	2.8	134
49	E1	1		748.9		1.1	709.9		78.4		1.4		9.5	6.5	1.5	14.1			2.7	131
50	E1	1		517.6		1.1	460.9		73.7		1.4	14.9		6.6	1.4		16.0		2.6	134
51	E1	1		487.7		1.3	370.0		77.2		1.6	18.3		7.3	1.9	13.8			3.0	133
52	E1	1		409.0		0.9	431.8		84.8		1.8	18.0		6.4	2.1	13.5			3.1	135
53 54	E1 E1	1 1		447.3 596.6		1.0 1.0	470.4 590.6		85.3 78.1		1.5 1.4	14.8 14.7		6.1 5.6	2.1 1.8	12.7	14.8		2.7 2.5	132 132
54 55	E1 E1	1		596.6 595.2		1.0	528.2		78.1 90.7		1.4	14.7			2.0	12.7				132
56	E1	1		807.9		1.1	791.2		90.7 88.0		1.5		9.9 9.6		1.3	12.7				132
57	E1	1		653.8		1.2	536.8		81.8		1.4		10.0		2.0	12.9			3.1	132
58	E1	1		533.8		1.1	496.1		81.3		1.7		7.6		1.8	13.8			2.5	135
59	E1	1	DH62	507.1	41.8	1.2	437.1	28.5	81.9		1.5		9.3		0.7	13.3			3.1	132
60	E1	1		507.0		1.6	313.6		84.0		1.4		10.1		1.1		16.0		3.2	131
61	E1	1		586.2		1.4	428.9		91.1				9.8		0.9	13.7			2.9	
62	E1	1	DH65	595.4	43.8	1.3	460.5	29.8	81.6	14.1	1.3	14.7	10.9	7.3	1.1	14.9	16.0	2.2	2.9	130

Table E.1 Continued.

No.	Env.	Rep.	Name	GYLD				TGW										SC GSP	HD
63	E1	1	DH66	354.2	40.0			34.0	87.6			19.5			2.9			2.5 2.4	134
64	E1	1	DH67	560.6	37.2		511.5	20 5		12.0		12.1			1.8			2.3 2.6	133
65 66	E1 E1	1 1	DH68 DH69	455.1 649.4	37.5 38.9		428.2 608.7	28.5 30.8	80.5 83.4	15.2		18.7 13.6			2.0 1.5			2.3 2.9 2.3 3.1	133 132
67	E1	1	DH70	633.5	36.6		544.2	32.5		12.5			10.3					2.3 2.6	132
68	E1	1	DH71	573.9	44.8		427.3	30.7	82.1			17.3			1.5			2.2 2.9	135
69	E1	1	DH72	578.3	43.3		469.4	30.5		14.8		18.4			1.6			2.4 2.7	137
70	E1	1	DH73	498.6	38.2	1.0	492.2	28.7	80.2	12.7	1.8	18.0	7.1	6.8	2.0	15.0	17.0	2.5 2.5	136
71	E1	1	DH75	614.6	36.6		500.1	34.3		12.2		12.6			1.9			2.2 2.8	130
72	E1	1	DH76	630.3	36.8		531.0	30.7		13.0		14.3			1.5			2.3 2.7	134
73	E1 E1	1	DH77	688.1 535.2	35.1		556.7 459.8	33.7		16.1 12.3			11.1		2.1 2.1			2.2 2.2	133
74 75	E1 E1	1 1	DH78 DH79	555.2 562.7	41.0 42.6		439.8	30.9 30.3	89.5			13.1 17.1			2.1			2.3 2.9 2.3 3.1	131 133
76	E1	1	DH80	657.8	42.4		502.1	30.6	90.5			17.4			1.9			2.5 2.8	135
77	E1	1	DH81	400.0	27.2		433.4	32.6	88.6			13.7			0.9			2.6 1.7	132
78	E1	1	DH82	644.4	36.6		626.9	31.8		11.9		14.9			1.9			2.3 2.7	130
79	E1	1	DH83	646.3	39.5	1.3	499.9	35.1	99.7	13.8	1.4	15.5	9.8	6.9	2.2			2.1 3.1	133
80	E1	1	DH84	669.3	34.7			37.4	90.5			11.1			1.8			2.1 2.8	130
81	E1	1	DH85	658.5	32.0		617.7	31.9	74.4				10.8					2.4 2.6	133
82	E1	1	DH86	648.8	43.0		500.2		92.6				9.2					2.5 3.1	131
83 84	E1 E1	1 1	DH87 DH89	435.7 630.0	41.7 34.6		383.2 570.1	27.8 32.3	85.5	14.1 11.4		14.5	12.3		1.6 2.5			2.4 2.9 2.6 2.4	133 134
85	E1	1	DH90	553.3	35.3		484.9	32.2	82.7			17.9			2.0			2.3 2.7	134
86	E1	1	DH91	668.0	36.0			31.5	95.6			17.9			2.5			2.5 2.6	131
87	E1	1	DH92	612.1	37.6			32.2	84.9			18.1			1.7			2.2 2.9	132
88	E1	1	DH93	539.2	46.4	1.3	406.0	30.1	76.9	12.3	1.4	13.3	9.1	7.0	1.5	14.6	16.1	2.3 3.2	130
89	E1	1	DH94	698.3	31.1	0.9	759.9	30.9	88.7			11.0	8.1		2.8	13.5	16.3	2.4 2.3	134
90	E1	1	DH95	751.8	35.3		581.9			11.3		11.5			1.8			2.1 2.6	130
91	E1	1	DH96	646.4	30.9		610.4	34.5	92.0				11.3					2.3 2.8	133
92 02	E1 E1	1 1	DH97	515.6 573.3	40.8		418.9 402.9	34.6	91.9			13.2 16.2			1.6			2.4 2.8	133
93 94	E1 E1	1	DH98 DH99	495.0	41.4 38.5			34.5 29.5	81.1 80.6			18.1			1.0 1.1			2.0 3.1 2.3 2.8	130 133
95	El	1	DH100		40.8		611.3	27.9	75.1			12.5			2.1			2.5 2.7	132
96	El	1	DH101		44.8		408.1	29.5		13.3			10.5					2.1 3.1	130
97	E1	1	DH102		42.5		518.4			14.5			10.0					2.4 2.7	133
98	E1	1	DH103	461.5	36.1	1.1	436.2	29.7	78.9	13.7	1.7	18.0	8.3	6.6	2.1	13.6	15.7	2.4 2.7	137
99	E1	1	DH104		41.1			27.9	90.3				10.9					2.6 2.6	136
100		1	DH105		41.6		581.5	28.2	81.3				10.3					2.6 3.1	135
101 102		1	DH106 DH107		39.5		372.6		85.4			18.8 12.6		7.0	2.1 1.6			2.5 2.5	135
102		1 1	DH107 DH108		37.0 33.0		556.2 475.6	29.4	84.7 92.2	11.5		12.0			2.4			2.2 2.8 2.5 2.5	130 132
103		1	DH109		36.6		507.7	29.4		12.3		14.6			2.4			2.3 2.3 2.7	132
105		1	DH110		37.3		393.1	29.4	92.3			15.4			2.0			2.2 2.5	133
106		1	DH111		46.6		361.9	28.9		16.6			10.9					2.2 3.1	133
107	E1	1	DH112	621.1	38.9	1.1	561.6	30.5	87.7	11.7		11.6			2.0			2.3 2.7	133
108		1	DH113				446.7		91.2									2.4 2.8	
	E1	1	DH114		36.2		521.4		68.0									2.2 2.6	133
	E1	1	DH115 DH116		31.8		567.3		87.6				9.2					2.3 2.4	134
111	E1 E1	1 1	DH110 DH117		31.4 32.3		605.4 553.9		86.5 78.8				8.5 7.7					2.3 2.6 2.2 2.5	133 133
	E1	1	DH119		44.1		392.1		92.2				12.9					2.2 2.3 2.9	133
	El	1	DH120		32.7		689.3		89.0				10.2					2.5 2.5	135
115		1	DH121		36.9		537.8		81.5				9.7					2.5 2.6	137
116	E1	1	DH122		44.8	0.9	571.2	27.8	88.3	14.7	1.6	18.8	9.2	7.2	1.5	16.0	17.5	2.4 2.8	134
117		1	DH123		44.0		339.7		96.0				11.9					2.2 2.8	135
118		1	DH124		37.4		591.6		83.2				10.7					2.2 2.7	134
119 120		1	DH125		37.8		597.5 357.6		79.0 76.7				8.7 8.7					2.3 2.8	133
120		1 1	DH126 DH128		45.8 42.0		357.6 428.4		76.7 93.1			20.5						2.3 2.8 2.6 2.7	136 136
121		1	DH128 DH129		43.0		527.3		91.5				8.7					2.3 3.2	130
123		1	DH130		35.3		599.7		85.2				9.2					2.3 2.6	134
124		1	DH131		38.9		314.3		88.0				8.4					2.4 2.5	137

Table E.1 Continued.

No. I	Env.	Rep.	Name	GYLD	GPS	GWPS	SPSM	TGW	PHT	FLL	FLW	FLA	FLS	SL	SSN	FSN	TSN	SC	GSP	HD
125 I	E1	2	DH1	581.7	34.8	1.0	567.5	30.3	84.8	11.4	1.2	10.9	9.5	6.0	1.3	12.3	13.6	2.3	2.8	132
126 I		2	DH3	428.9	38.1		409.2	27.5	88.8	12.5		14.0		6.4			16.0			136
127 I		2	DH4	525.7	36.5		433.1	32.9	78.7	11.3		14.2		7.0			17.0			133
128 I		2	DH5	359.3	36.6		390.1	29.9	80.9	13.9		16.9		7.0			15.4			135
129 I		2	DH6	559.5	40.3		460.5	31.4	86.7	13.8			10.0				15.0			130
130 I 131 I		2 2	DH7 DH8	535.0 564.3	35.9		505.2 368.1	31.5 30.8	85.1 91.9	12.7 14.7		15.0	8.5 10.3	6.6 7.4			17.6 16.9			136 132
131 I 132 I		2	DH8 DH9	304.3 484.1	50.1 43.7		338.3	30.8 31.0	86.1	14.7		17.5		7.7			17.5			132
132 I 133 I		2	DH11		43.9		446.8	35.4	99.3	16.6			11.3				15.5			133
134 I		2	DH12		53.4		182.9	32.9	84.5	14.2		17.9		8.1			18.9			134
135 I		2	DH13		45.5		378.1	28.5	92.2	15.9			11.0				17.9			136
136 I	E1	2	DH14	634.0	32.4	1.1	590.9	32.4	89.4	14.1	1.6	17.6	8.9	6.6	3.2	13.5	16.7	2.5	2.4	135
137 I	E1	2	DH15	647.9	37.2	1.2	553.3	31.9	82.8	13.6	1.4	15.4	9.5	7.2	1.7	14.2	15.9	2.2	2.6	130
138 I		2	DH16		41.6		493.5	30.8	82.6	12.8		14.2			1.6	13.5	15.1	2.4	3.1	132
139 I		2	DH17		45.9		349.0	34.4	88.8	16.3			10.1				16.7			130
140 I		2	DH18		43.4		289.6	32.1	85.2	12.2		15.7		7.5			17.9			135
141 I		2	DH19		38.5		286.6	32.1	87.4	12.8		15.2			1.5		15.1			132
142 I		2	DH20		38.0		490.2	29.7	81.8	13.8		17.6		7.0			16.2			134
143 H 144 H		2 2	DH21 DH22		36.8 48.9		523.0 347.9	33.6 32.5	90.4 93.7	14.3 13.8		16.8 16.2			2.7 1.4		15.6 17.3			135 135
144 I 145 I		2	DH22 DH23		45.4		466.6	31.6	93.7 93.7	14.9			10.9				14.6			130
146 I		2	DH24		42.2		587.1	31.9	88.7	14.7		19.1		6.8			15.0			132
147 I		2	DH25		48.3		508.7	34.2	84.3	14.0		16.6			1.6		17.3			132
148 I		2	DH26		38.1		444.0	32.3	78.0	12.1		13.3			1.6		16.0			133
149 I	E1	2	DH27	575.2	39.9	1.2	483.8	28.3	92.9	13.5	1.5	15.9	9.1	6.4	2.3	13.4	15.7	2.5	3.0	136
150 I	E1	2	DH28	588.7	38.7	1.2	493.5	33.0	91.5	15.4	1.6	19.2		6.3			16.1			134
151 I		2	DH29		37.1		348.9	31.9	75.9	14.0			10.0				17.1			133
152 I		2	DH30		42.2		448.2	35.4	93.3	13.9		17.7		6.7			17.6			133
153 I		2	DH31		46.8		340.2	29.1	83.0	12.5		15.2		7.6			16.6			134
154 H 155 H		2 2	DH32		37.6 48.7		568.8	27.2	80.2 90.4	11.1		13.5 23.8		7.2 7.2			17.8			138 136
155 I 156 I		2	DH33 DH34		46.8		391.7 425.8	29.7 33.5	90.4 97.4	17.1 14.5		25.8 17.4			2.0 1.5		18.2 16.9			130
150 I		2	DH35		36.1		438.9	34.0	83.5	10.9		12.9		7.0			15.8			134
158 I		2	DH36		49.9		294.3	31.9	83.0	14.6		19.7		8.6			18.5			134
159 I		2	DH37		33.6		516.6	30.5	84.9	16.0			10.5				15.7			134
160 I	E1	2	DH38	669.5	43.7	1.4	479.6	31.4	80.4	15.5	1.6	19.0	10.1	7.2	1.0	14.6	15.6	2.2	3.0	130
161 I	E1	2	DH39		37.2	1.1	460.2	31.0	89.0	11.7	1.3	12.4	8.8	6.2	2.5	14.8	17.3	2.8	2.5	135
162 I		2	DH40		42.8		351.9	32.9		13.5			10.6				16.9			133
163 I		2	DH41		41.2		573.8	30.0	87.7	13.3		14.7		7.0			15.7			135
164 I		2	DH42		41.0		340.2	30.5	87.3	14.7			11.3				17.3			136
165 I		2	DH43		41.6		458.3	31.8	84.5	12.8		14.6		7.0			15.7			134
166 I 167 I		2 2	DH44 DH45		41.7 36.4		397.8 450.9	34.9 35.8	95.4 89.1	15.4 11.4		18.5	10.2	7.9			16.7 16.4			133 132
167 I		2	DH46		43.0		277.4	31.4	89.5	17.2			10.4				16.4			132
169 I		2	DH47		36.5		676.4	32.7	91.7	13.6		17.3			1.5		15.5			133
170 I		2		1091.6			699.7	32.0	92.8	15.1			9.9		1.9		17.0			134
171 I	E1	2	DH50		41.9		490.0	35.6	96.4	14.3	1.6	17.8	9.1	7.1	1.5		15.6			130
172 I		2	DH51	480.2	41.2	1.0	461.7	28.8	88.5	15.5	1.5	18.4	10.3	7.2	2.5	13.9	16.4	2.3	3.0	134
173 I	E1	2	DH52		39.3		547.4	29.0	80.9	12.9			10.3				15.7			132
174 I		2	DH53		30.3		816.8	30.3	73.5	10.5			8.0				17.1			134
175 I		2	DH54		45.5		244.7	32.7	83.0	16.5			10.6				16.2			137
176 I		2	DH55		35.4		593.9	28.7	91.8	11.3		12.3		6.1			15.5			134
177 H 178 H		2 2	DH56 DH57		31.7 31.8		657.9 535.8	31.7 29.3	90.2 84.7	12.3 14.0		13.9 16.2		6.0 5.8			14.8			133 136
178 I 179 I		2	DH57 DH58		43.9		378.3		84.7 84.7	14.0			9.0 8.9				15.3 14.9			130
180 I		2	DH59		43.7		599.0	32.7	83.2	14.3			10.3				15.2			130
181 I		2	DH60		46.4			31.9	83.5	14.8			11.3				15.5			132
182 I		2	DH61		35.6			31.5	84.8	12.8			8.1				15.6			136
183 I		2	DH62		40.6		462.4		87.0	14.2		15.6	10.3	6.4	1.1		14.4			132
184 I		2	DH63	631.4	48.3	1.6	398.1	33.2	87.0	15.6	1.6		10.0			15.1	16.5	2.1	3.2	131
185 I		2	DH64		43.0		306.9		96.1	13.3			9.2				15.8			132
186 I	E1	2	DH65	519.6	50.3	1.5	342.7	30.8	85.4	15.9	1.4	17.9	11.1	7.6	1.0	15.5	16.5	2.2	3.2	130

Table E.1 Continued.

No.	Env.	Rep.	Name	GYLD	GPS GWPS	SPSM	TGW	PHT	FLL	FLW	FLA	FLS	SL	SSN	FSN	TSN	SC	GSP	HD
187	E1	2	DH66	396.9	45.6 1.6	245.6			13.5		18.6		7.9			19.0		2.8	136
188	E1	2	DH67	628.9	36.6 1.2	518.4			12.8		14.4		7.0			16.0		2.6	131
189 190	E1 E1	2 2	DH68 DH69	454.5 487.0	37.9 1.3 37.4 0.9	358.4 532.2	27.5 30.1		16.3 12.1		21.7 12.1		7.1 6.0			16.0 14.6		2.8 2.9	133 133
190	E1 E1	2	DH09 DH70	487.0 505.3	42.4 1.5		32.5		12.1		12.1		7.8			14.0		2.9	133
192	E1	2	DH71	625.7	45.9 1.4	437.9			13.4		16.7		8.0			17.4			134
193	E1	2	DH72	564.8	42.7 1.4		30.9		13.1		15.3		7.4			17.8		2.6	135
194	E1	2	DH73	549.0	43.0 1.3	413.4	29.6	90.0	11.7	1.4	13.4	8.1	7.2	1.7	15.5	17.2	2.4	2.8	136
195	E1	2	DH75	655.8	39.9 1.5	446.7			13.4		16.2		7.5			16.0		2.8	130
196	E1	2	DH76	721.4	35.4 1.1	637.8			13.2			9.7	6.4		12.8			2.8	134
197 198	E1 E1	2 2	DH77 DH78	601.8 608.0	30.5 1.1 47.6 1.4	570.4 445.4			14.3 13.8			11.2 10.0				17.5 17.8		2.0 2.9	133 133
199	E1	2	DH79	644.7	45.2 1.3	511.3			13.2			9.7				16.4		3.2	133
200	E1	2	DH80	611.0	46.4 1.4	443.4	30.7		15.1			11.1		1.6		17.8		2.9	135
201	E1	2	DH81	418.2	41.4 1.4	303.7		87.3	11.8	1.4	13.1	8.5	6.8		15.8	17.1	2.5	2.6	132
202	E1	2	DH82	563.9	45.0 1.6	357.6				1.4	10.9		7.8			19.0		2.7	133
203	E1	2	DH83	764.8	38.0 1.3	569.0		100.6			18.4		7.0			15.4			133
204 205	E1 E1	2 2	DH84 DH85	834.4 738.8	32.8 1.2 28.6 0.9	694.1 863.0			10.2 14.3		9.6 16.7	8.6	6.9 6.0			14.7 14.7		2.6 2.3	130 134
205	E1	2	DH85 DH86	607.3	53.8 1.7	352.1			12.1		13.1		6.9			15.8		3.6	132
207	E1	2	DH87	581.1	54.4 1.6	367.8			13.2			10.9				16.7		3.3	131
208	E1	2	DH89	624.2	35.2 1.2	520.6	33.9	88.4	12.7	1.5	15.1	8.4	6.5	2.4	13.7	16.1	2.5	2.6	133
209	E1	2	DH90	735.5	33.4 1.0		34.1		13.4		16.9		6.5			15.6		2.5	130
210	E1	2	DH91	607.4	36.3 1.2		33.1		13.7		15.1		6.4			15.1		2.8	133
211 212	E1 E1	2 2	DH92 DH93	450.4 484.6	44.1 1.3 43.9 1.2	357.8 391.8	32.9		15.0 12.6		17.8	10.1	7.1 7.0			15.6 16.4		3.1 3.0	133 130
212	E1	2	DH93	580.9	34.1 1.1		30.2		12.0		11.3		7.0			16.9		2.3	130
213	E1	2	DH95	528.3	32.9 1.2	452.7			14.1		17.1		7.2			15.6			130
215	E1	2	DH96	828.3	38.8 1.4	603.7	37.3		13.3		15.1		6.4			14.5		3.1	133
216	E1	2	DH97	476.8	47.3 1.6	300.6			10.9		13.1		7.1		15.2			3.1	133
217	E1	2	DH98	566.6	46.1 1.6	351.3			12.2		15.3		7.6			15.6		3.1	130
218 219	E1 E1	2 2	DH99 DH100	438.9	44.2 1.3	350.0	29.6 28.6		13.3 11.4		16.6 12.3		7.1	1.4		16.3	2.3	3.0	135 133
219	E1	2	DH100 DH101		42.7 1.3	480.5	31.4		12.2		14.5		7.2	1.1	14.5	15.6	2.2	2.9	132
221	E1	2	DH102		50.8 1.4		28.9		13.8		15.3		8.3			18.1		3.1	134
222	E1	2	DH103		36.4 1.1	367.7	30.8		12.8		15.9		6.6			15.4		2.8	136
223	E1	2	DH104		36.9 1.0	412.8			15.0			11.2				17.2		2.4	135
224 225	E1 E1	2 2	DH105 DH106		41.6 1.1	495.9 407.8	27.9		14.2		16.1 14.7		6.2			17.0		2.9	134
223	E1 E1	2	DH100 DH107		45.2 1.4 39.9 1.2	407.8			11.9 13.0		14.7		7.3 7.0			17.3 14.9		2.9 3.0	133 132
227	E1	2	DH108		40.8 1.2	407.6			11.9		13.1		7.0			16.9		2.7	132
228	E1	2	DH109		39.3 1.2	496.0	30.1		14.0		16.0		7.1			15.9		2.9	133
229	E1	2	DH110		46.5 1.4	339.5	31.8		13.2			10.0				17.2		3.0	132
230	E1	2	DH111		54.8 1.7	294.1	30.2		15.7			11.3				17.9		3.2	133
231 232	E1 E1	2 2	DH112 DH113		46.6 1.4 39.6 1.3	361.3 427.9	31.2		12.1 12.0		13.7	8.5 9.4	7.7			16.7 15.8		3.1 2.8	132 132
232		2			38.5 1.3	486.5		72.1						1.1					
234		2			32.7 1.0	503.4		93.7						2.1					
235	E1	2			31.0 1.0	537.5			11.0		12.8				12.2				131
236	E1	2	DH117		35.2 1.2	452.0			12.6					1.4					133
237	E1	2			46.4 1.5	333.3			15.0		19.5				15.4				136
238 239	E1 E1	2 2	DH120 DH121		36.8 1.1 36.8 1.2	365.1 501.9			13.1 12.9		15.1 14.5				14.5 15.1				135 135
239 240	E1 E1	2	DH121 DH122		49.3 1.4	242.8			14.5		14.5					17.4		2.4 3.0	135
240	El	2	DH122 DH123		36.6 0.9	312.4			14.6		15.0				13.9				136
242	E1	2	DH124	515.3	33.0 0.9	548.8	29.9	87.3	14.1	1.5	16.4	9.7	7.0	2.2	13.0				135
243	E1	2			40.6 1.5	511.5			12.4		16.6				15.0				134
244	E1	2	DH126		51.5 1.5	265.6			12.3		15.2				17.2				135
245 246	E1 E1	2 2	DH128 DH129		45.5 1.2 42.6 1.4	292.5 472.7		90.4 91.3	19.2 12.7		21.0			1.9 1.8	15.8				137 132
240 247	E1 E1	2			42.0 1.4 46.7 1.4	472.7		91.5 82.2						1.8					132
248		2			38.4 1.3			85.7						1.7					

Table E.1 Continued.

No.	Env.	Rep	. Name	GYLD	GPS	GWPS	SPSM	TGW	PHT	FLL	FLW	FLA	FLS SL	SSN	FSN	TSN SC	GSP	HD
249	E2	1	DH1	938.1	29.8	0.8	1175.6	26.8	94.3	14.6	1.3		10.9 6.7			16.6 2.5		141
250 251	E2 E2	1 1	DH3 DH4	782.8 798.0	36.8 32.7	1.1	734.3 866.5	29.1 30.3	92.8 84.6	13.6 13.8	1.5 1.5		9.3 6.9 9.3 7.2			17.1 2.5 18.7 2.6		141 143
251		1	DH4 DH5	798.0		0.9 0.8	863.5	26.6	84.0 78.7	15.8	1.5		9.5 7.2			16.4 2.2		143
253	E2	1	DH5 DH6	885.5	36.0	0.8	936.1	30.3	97.6	16.4	1.4		11.9 7.3			17.7 2.4		142
254		1	DH7	865.4	35.6	1.0	866.3	32.0	87.7	14.8	1.5					17.8 2.6		143
255	E2	1	DH8	888.0	38.6	1.1	805.0	30.3	99.8	16.4	1.4	18.7	11.4 7.5	2.3	15.2	17.5 2.3	2.2	140
	E2	1	DH9	761.4	38.0	1.0	770.7	31.9		16.1	1.6		9.9 7.7			19.6 2.6		144
257		1	DH11	817.9	38.4	1.3	651.7	32.3	107.9		1.3		11.9 8.3			17.5 2.1	2.2	142
258		1	DH12		35.7	1.0	690.9	29.2		15.0	1.7		9.1 6.8			16.9 2.5		143
259 260	E2 E2	1	DH13 DH14	807.1 823.6	35.6	0.9 0.9	899.8 898.1	26.9 31.5	89.7 87.9	18.9 16.9	1.4 1.4		13.1 7.5 12.5 7.1			19.8 2.7 17.9 2.5		142 143
260	E2 E2	1	DH14 DH15	900.7		0.9	1120.2	28.9		16.2	1.4		11.4 7.0			16.4 2.4		143
	E2	1	DH16	752.6		1.0	739.3	28.3	89.3	14.0	1.5		9.3 7.0			16.4 2.4		142
263	E2	1	DH17	839.2		1.1	768.5	32.7	89.6	17.8	1.5		12.2 7.4			16.5 2.2		140
264	E2	1	DH18	793.3	39.1	1.1	730.5	31.1	81.6	17.6	1.9	26.6	9.3 7.6	1.7	15.8	17.5 2.3	2.2	145
265	E2	1	DH19	822.2		1.0	855.6	32.3	92.6	14.3	1.4		10.3 6.6			15.5 2.3		140
266	E2	1	DH20	810.2		1.0	775.3		88.0	15.3	1.6		9.5 7.1			18.2 2.6		144
267		1	DH21	836.3		1.0	812.7	32.9		18.1	1.5		12.5 7.4			17.7 2.4		
268 269	E2 E2	1 1	DH22 DH23	849.6 884.2	34.1 33.3	0.9 0.9	923.4 963.2	31.8 28.1	97.1 92.5	16.7 18.7	1.5 1.4		11.2 7.6 13.7 6.3			18.9 2.5 16.1 2.5		143 141
209	E2 E2	1	DH25 DH24	909.7	33.9	0.9	1042.0	28.4	92.5 95.3	15.6	1.4		9.6 6.7			16.3 2.4		141
271	E2	1	DH25		34.1	0.9	973.3	30.5		16.0	1.3		11.9 7.3			17.7 2.4		139
272	E2	1	DH26	862.1	34.5	0.9	956.8	29.1	85.7	17.7	1.4		12.3 7.2			17.5 2.5		142
273	E2	1	DH27	975.6	30.8	0.9	1142.4	28.9	99.2	17.7	1.4	19.4	12.9 6.2	2.4	13.7	16.1 2.6	1.9	144
274		1	DH28	895.4	36.8	1.0	927.9	29.7	96.9	15.4	1.4		11.1 7.1			17.7 2.5		143
275	E2	1	DH29		34.9	0.9	897.9	30.0		15.3	1.4		10.9 7.4			17.4 2.4		143
276	E2	1	DH30		31.6	1.1	780.8	34.1		18.3	1.4		12.7 7.0			18.1 2.6		142
277 278	E2 E2	1	DH31 DH32	679.8 780.3	32.5 30.8	0.7	921.1 1005.6	26.7	87.2 86.9	14.6	1.4		10.1 7.3			16.9 2.3 17.6 2.7	1.9	141 145
278	E2 E2	1	DH32 DH33	644.6		0.8 0.8	799.7	26.4 26.9	86.9 96.2		1.4 1.5		8.8 6.5 10.3 7.3			20.2 2.8		143 147
280	E2	1	DH35 DH34	837.0	37.3	1.0	798.7	28.8	100.2		1.4		11.5 7.6			18.2 2.4		141
281	E2	1	DH35	867.5		0.8	1135.5	30.9	91.9		1.5		10.0 7.1			16.9 2.4		141
282	E2	1	DH36	862.0	33.4	0.9	909.5	29.3	83.5	18.9	1.7		11.0 7.8			18.1 2.3		142
283	E2	1	DH37	693.3	33.2	0.8	855.9	26.4	90.2	16.0	1.3	16.4	12.4 7.4			18.5 2.5	1.8	141
284		1	DH38	805.7		0.9	883.4	27.3	86.5		1.4		11.3 7.2			17.8 2.5		
285	E2	1	DH39	932.9	36.3	1.1	882.6	29.4	87.4		1.3		12.2 6.4			17.6 2.7		140
286 287	E2 E2	1 1	DH40 DH41	760.5 873.5	33.5 31.3	1.0 0.9	780.0 922.4	30.6 31.6	100.8 89.9	14.9	1.3 1.4		11.5 7.8 11.6 7.1			17.8 2.3 18.1 2.6	1.9	142 144
287	E2 E2	1	DH41 DH42		35.3	0.9	922.4	29.7	89.9 90.3	18.9	1.4		13.5 7.5			18.1 2.0		144
289	E2	1	DH42 DH43	934.0	36.6	1.1	879.5	32.0	90.6	16.3	1.4		11.4 7.3			17.0 2.3	2.2	142
290	E2	1	DH44	940.9	30.6	0.9	999.9	33.0	109.3		1.5		10.7 7.4			17.1 2.3	1.8	145
291	E2	1	DH45	927.1	32.1	1.1	868.8	33.2	97.8	14.8	1.5	18.0	9.7 7.8	2.4	15.6	18.0 2.3	1.8	143
292	E2	1	DH46	722.9	31.8	0.6	1147.5	28.8	94.3	17.8	1.5		11.5 7.7			18.2 2.4	1.7	145
293	E2	1	DH47	831.5	34.4	1.0	835.7	31.0	92.8	14.2	1.4		10.1 7.1	2.4		17.2 2.4		142
294	E2	1	DH49		39.3	1.0	771.5	30.8	91.6		1.7		10.9 7.5			18.0 2.4		145
295	E2 E2	1	DH50	889.9 725.8	30.6	0.9	989.8 917.6	30.3	104.4		1.4		10.2 6.9			17.4 2.5 18.6 2.4		143
290		1	DH51 DH52			0.8 0.8	1123.9		83.0							16.8 2.5		
298		1	DH52 DH53	914.3		1.1	860.9	26.9		16.6						17.8 2.5		142
	E2	1	DH54	881.7		1.2	723.9	31.9		19.5						17.7 2.1		
300	E2	1	DH55	801.1		0.9	855.8	26.7	92.2		1.5	17.4	10.3 6.5	2.3	14.4	16.7 2.6	2.1	139
301	E2	1	DH56	959.7	29.0	0.9	1026.4	32.2	87.3	17.7	1.4	20.2	12.2 6.6	2.6	14.0	16.6 2.5	1.7	143
	E2	1	DH57	892.0		1.0	938.9	27.2	93.8		1.5					18.0 2.7		
	E2	1	DH58	683.4		0.8	898.0	30.5	94.3		1.4					15.3 2.4		
304 305		1	DH59	910.8		0.9	961.8	26.6		13.6						16.7 2.5		
	E2 E2	1 1	DH60 DH61	983.9 870.6		1.1 0.8	903.4 1151.6	30.0 29.1	90.5 89.7							17.3 2.3 17.4 2.3		
	E2 E2	1	DH62	838.3		1.1	753.8	29.1	92.0		1.3					17.4 2.3		
	E2	1	DH63	885.1		1.1	764.3	29.6	84.0		1.7					18.1 2.2		
309		1	DH64	857.5		1.2	719.4		100.2							17.3 2.2		
310	E2	1	DH65	826.8	38.9	1.0	863.9	26.8	87.8	18.6	1.3					19.4 2.5		

Table E.1 Continued.

No.	Env.	Rep.	Name	GYLD	GPS	GWPS	SPSM	TGW	PHT	FLL	FLW	FLA	FLS	SL	SSN	FSN	TSN	SC	GSP	HD
311		1	DH66	740.2	34.8	1.0	746.9	34.3	92.6	16.5		22.2	9.7		3.4	15.8	19.2	2.4		145
312		1	DH67	676.6	31.0		890.2	28.0	85.9	16.4			11.6				17.2			139
313		1	DH68	600.8	33.7		717.8	26.2	77.4	15.8			10.6				16.5			141
314		1	DH69	823.4	37.7		961.9	30.8	91.3	14.8			10.4				16.8			141
315 316		1 1	DH70 DH71	911.0 707.0	35.4 39.8		891.3 653.5	31.8 29.2	90.3 86.1	16.8 16.4			11.2 11.2				19.2 17.3			144 144
317		1	DH72	835.5	36.8		985.3	30.7	85.1	14.4			9.3	7.5			17.5			144
318		1	DH72 DH73	832.5	38.8		880.0	31.2	91.5	16.4		21.8		7.6			19.2			145
319		1	DH75	901.8	33.2		971.7	33.5	97.3	18.0			13.2				17.5			142
320	E2	1	DH76	837.7	30.6		1035.5	28.7	84.5	17.1	1.4	19.8	11.8	6.8	2.6		16.8			142
321	E2	1	DH77	926.0	32.7	0.9	1007.7	31.9	94.0	18.3	1.4	20.0	13.4	8.5	3.2	16.9	20.1	2.4	1.5	141
322	E2	1	DH78	764.6	35.8	0.9	849.6	28.3	88.0	14.4	1.3	14.7	11.2	7.4	2.5	15.6	18.1	2.5	2.0	140
323		1	DH79	776.5	35.5		785.1	30.2	92.9	16.9		17.8	12.7				16.6			141
324		1	DH80	873.5	38.9		766.2	29.2	87.4	17.1			12.5				17.1			140
325		1	DH81	711.7	37.6		639.9	30.8	90.9	15.0			10.6				17.9			141
326		1	DH82	730.8	37.6		767.6	27.5	91.2	13.5			9.8		1.7		17.1			140
327 328		1 1	DH83 DH84	986.3 997.7	30.4 29.8		971.8 1111.0	35.8 31.0	98.2 87.0	16.3 16.6		22.4 17.8	9.5 12.3		3.2		16.7 15.5			143 140
329		1	DH85	864.6	31.0		1026.8		87.5	15.7			12.5				17.8			140
330		1	DH85 DH86	698.5	31.8		804.7	29.7	95.9	14.7			11.0					2.6		142
331		1	DH87	978.5	36.6		1038.7		89.6	17.2			12.2				16.6			139
332	E2	1	DH89	829.1	29.3		937.9	32.2	93.6	14.8			10.0				17.8			143
333	E2	1	DH90	867.5	33.6	1.0	882.5	29.6	86.1	16.6	1.5	19.4	11.3	7.4	3.0	15.2	18.2	2.4	1.9	140
334	E2	1	DH91	809.0	36.2	1.0	803.4	29.5	92.8	17.1	1.4		12.6				17.6			141
335		1	DH92	865.5	31.8		966.0	29.8	84.8	16.8			11.2				18.1			144
336		1	DH93	877.7	39.8		853.8	•	86.1	17.7			12.6				18.7			140
337		1	DH94	849.3	29.6		962.9	31.4	100.1					7.2			17.9			142
338		1	DH95	839.4	35.3		803.2	33.2	88.1	14.9			10.0 11.1				16.8			140
339 340		1 1	DH96 DH97	1089.0 879.3	31.8 34.9		1030.2 881.0	34.5 32.4	102.2 88.0	14.9		15.8 19.3			2.5 2.0		15.9 17.3			141 141
340		1	DH97 DH98	879.5	35.5		738.3	33.0	92.0	16.9			11.6				15.9			139
342		1	DH99	751.5	40.5		703.0	28.7	85.5	14.9		18.9		7.5			17.3			143
343		1		815.5	42.2		910.2	25.0	80.2	14.4			10.0				18.6			140
344	E2	1	DH101	844.9	39.2	1.0	855.2	26.5	94.4	13.4	1.4	14.6	9.8	7.4	1.6	15.7	17.3	2.3	2.3	142
345	E2	1	DH102	822.3	39.7	0.9	880.4	27.7	99.0	15.6	1.5	18.9	10.2	7.7	3.0	16.1	19.1	2.5	2.1	145
346		1	DH103		32.3		677.8	30.1	85.2	14.6			8.7				17.3			146
347		1	DH104		41.3		777.3	28.1	98.3	16.5			11.7				18.4			144
348		1	DH105		33.0		850.8	27.5	86.2	15.4			11.2				17.0			141
349 350		1 1	DH106 DH107		40.9		840.4 1079.2	29.0	93.4 97.2	16.2 12.7			10.4	8.0 7.0			18.8 15.9			142 140
350		1	DH107 DH108		31.2 29.7		1079.2	29.0	97.2 87.0	12.7		12.9	9.8 11.8				16.8			140
352		1	DH109		34.7		897.1	26.9	91.0	16.2			11.5				18.0			143
353		1	DH110		38.7		802.4	28.0	101.2				10.1				18.8			140
354		1	DH111	680.8	38.3		684.3	27.7	93.3	17.2		18.8	12.4				17.8			140
355	E2	1	DH112	777.1	40.0	1.0	749.4	28.0	91.6	15.6	1.4	17.8	10.9	7.8	2.0	16.6	18.6	2.4	2.1	141
356	E2	1	DH113	821.5	32.3	0.9	885.2	29.7	99.0	16.1	1.4		11.5				16.5			141
357		1	DH114		38.9		739.7	28.3	80.0	16.5			11.0				16.8			142
358		1	DH115		27.2		1097.6		99.1	13.1			9.0				17.5			141
359		1	DH116		25.0		1002.0		94.2	13.4			10.3				16.0			142
360		1	DH117		32.4		997.2	30.1	87.1	15.7			10.6				15.9			141
361 362		1 1	DH119 DH120		34.4 28.4		752.0 1197.0	31.8	90.6 83.4	17.2 18.2			10.6 13.7				18.1 17.2			143 142
363		1	DH120 DH121		30.7		807.7	30.0	81.8	16.1			11.0				18.6			142
364		1	DH121 DH122		34.2		1088.7		99.1	16.7			11.0				16.3			146
365		1	DH123		35.6		809.9	26.0	94.1	17.5			13.9				18.8			144
366		1	DH124		36.5		907.1	28.3	85.4	17.8			12.4	8.0	2.3		18.1			144
367	E2	1	DH125	808.3	32.4		911.3	28.0	86.5	13.5		15.1		7.0			16.3			140
368		1	DH126		39.2			26.2	81.5	14.4			9.8				17.2			142
369		1	DH128		29.2		1115.5		94.2	19.4			15.6				17.3			142
370		1	DH129		36.9		679.8	28.3	96.2	12.7			10.2				17.0			140
371		1	DH130		36.0		908.5	29.6	89.3	14.8			10.0				17.6			141
372	EΖ	1	DH131	000.3	30.9	1.0	721.7	34.7	90.6	18.8	1./	24.9	11.5	1.8	4.0	13.3	19.5	2.3	1.0	145

Table E.1 Continued.

No.	Env. Rep	. Name GYLD GPS	GWPS SPSM	TGW PHT	FLL FLW	FLA FLS SL	SSN	FSN TSN SC	GSP HD
373	E2 2	DH1 929.6 38.8		26.6 93.1	15.2 1.3	16.1 11.4 7.3	1.4	15.6 17.0 2.3	2.5 141
374	E2 2	DH3 804.7 37.5		30.2 92.6	14.5 1.5	17.1 9.7 6.8	1.8	15.0 16.8 2.5	2.5 142
375	E2 2	DH4 693.9 29.3		29.4 80.2 27.9 82.7	15.7 1.6	19.9 9.7 7.0	3.2	15.0 18.2 2.6	1.9 144
376 377	E2 2 E2 2	DH5 684.8 40.5 DH6 773.9 38.1		27.9 82.7 29.4 90.4	14.0 1.5 14.1 1.3	16.1 9.6 8.0 14.6 10.8 7.2	1.4 1.7	15.8 17.2 2.2 15.3 17.0 2.4	2.6 141 2.5 140
378	E2 2	DH7 718.7 37.0		32.5 81.1	15.7 1.5	19.5 10.1 7.1	2.8	15.3 18.1 2.6	2.4 143
379	E2 2	DH8 695.1 41.0		27.7 85.8	14.8 1.4	16.0 10.8 7.5	1.7	15.0 16.7 2.2	2.7 141
380	E2 2	DH9 636.5 36.4			15.7 1.5	19.2 10.3 7.1	2.7	15.1 17.8 2.5	2.4 142
381	E2 2	DH11 977.2 39.4			5 15.2 1.2	14.9 12.3 8.7	1.5	16.3 17.8 2.0	2.4 141
382 383	E2 2 E2 2	DH12 586.9 38.7			12.7 1.8	17.5 7.2 6.4	1.2	15.2 16.4 2.6 17.5 19.1 2.5	2.5 142
383 384	E2 2 E2 2	DH13 577.5 44.0 DH14 878.4 33.7		25.0 82.1 32.3 87.5	15.0 1.3 17.6 1.5	15.4 11.6 7.6 21.1 11.6 7.5	1.6 2.5	17.3 19.1 2.3	2.5 141 2.1 143
385	E2 2	DH14 878.4 35.7 DH15 813.8 31.2		28.0 87.3	14.4 1.3	15.2 10.8 7.1	1.9	14.6 16.5 2.3	2.1 143
386	E2 2	DH16 732.6 30.1		28.5 87.5	14.8 1.5	17.5 10.0 6.7	3.1	13.3 16.4 2.5	2.3 142
387	E2 2	DH17 730.2 39.1	1.3 567.8	33.1 89.6	16.0 1.4	17.6 11.5 7.7	2.0	15.2 17.2 2.2	2.6 139
388	E2 2	DH18 781.5 40.2		30.7 89.4	14.4 1.9	21.7 7.6 7.8	2.4	16.2 18.6 2.4	2.5 146
389	E2 2	DH19 738.5 34.5		30.3 78.4	14.5 1.3	15.3 10.8 6.5	1.6	13.3 14.9 2.3	2.6 139
390 391	E2 2 E2 2	DH20 739.5 41.9 DH21 822.5 31.6		28.8 80.8 31.8 90.6	16.8 1.6 15.1 1.4	21.9 10.2 7.4 16.3 11.1 7.2	2.0 3.2	16.1 18.1 2.5 14.0 17.2 2.4	2.6 143 2.3 142
392	E2 2 E2 2	DH21 822.5 51.6 DH22 847.0 42.5			15.4 1.5	17.8 10.6 8.0	1.6	17.5 19.1 2.4	2.3 142
393	E2 2	DH23 820.1 39.4		27.0 91.8	17.0 1.3	17.4 13.3 6.6	1.7	14.6 16.3 2.5	2.7 141
394	E2 2	DH24 880.0 37.4	1.1 820.9	28.7 85.3	15.4 1.5	17.9 10.5 7.0	1.3	14.7 16.0 2.3	2.5 141
395	E2 2	DH25 705.3 36.2		29.3 78.5	13.5 1.3	13.9 10.3 7.0	2.2	15.3 17.5 2.5	2.4 138
396	E2 2	DH26 815.4 35.5		29.4 82.1	14.8 1.5	17.1 10.1 7.0	1.9	14.9 16.8 2.4	2.4 141
397 398	E2 2 E2 2	DH27 667.1 34.9 DH28 729.9 32.7		30.287.230.187.6	13.8 1.2	13.4 11.2 6.4 13.5 10.6 6.5	1.8 2.0	14.0 15.8 2.5 13.7 15.7 2.4	2.5 141 2.4 141
399	E2 2 E2 2	DH29 816.7 31.0		28.7 81.4	13.4 1.3 12.9 1.4	13.9 9.5 7.1	2.0	15.0 17.5 2.5	2.4 141 2.1 141
400	E2 2	DH29 810.7 51.0 DH30 893.2 31.8		35.4 90.9	16.9 1.5	20.4 11.1 7.2	2.5	15.9 18.4 2.6	2.0 143
401	E2 2	DH31 632.8 36.3			14.9 1.4	16.2 10.9 7.4	1.7	15.1 16.8 2.3	2.4 140
402	E2 2	DH32 863.6 31.2			14.0 1.4	15.5 10.0 6.6	3.1	14.8 17.9 2.7	2.1 146
403	E2 2	DH33 731.3 43.5		27.3 93.6	18.8 1.7	25.6 11.0 7.7	2.8	17.4 20.2 2.6	2.5 147
404 405	E2 2 E2 2	DH34 733.0 42.8 DH35 752.0 34.3		28.5 95.3 30.9 88.2	15.3 1.4	17.0 10.8 7.7 14.5 9.9 7.2	1.5 2.2	16.9 18.4 2.4 14.7 16.9 2.4	2.5 141 2.3 141
403	E2 2 E2 2	DH35 752.0 34.3 DH36 867.6 37.0		30.9 88.2 29.3 84.3	13.4 1.4 17.6 1.7	23.0 10.6 8.4	2.2	16.9 19.2 2.3	2.3 141 2.2 143
407	E2 2	DH37 708.0 40.6		25.2 90.3	15.2 1.4	16.5 11.2 7.5	2.2	16.4 18.6 2.5	2.5 141
408	E2 2	DH38 995.7 37.4		27.1 82.9	14.8 1.4	16.2 10.8 7.4	2.2	16.2 18.4 2.5	2.3 141
409	E2 2	DH39 1098.1 31.6			18.5 1.4	20.7 13.3 6.3	3.0	14.6 17.6 2.8	2.2 140
410	E2 2	DH40 744.0 36.5			12.8 1.2	12.6 10.4 8.2	2.0	17.0 19.0 2.3	2.1 143
411 412	E2 2 E2 2	DH41 696.9 33.4 DH42 918.7 43.5		26.8 85.2 29.6 94.3	13.0 1.2 16.1 1.3	13.0 10.4 7.0 17.1 11.9 7.9	1.9 1.4	15.0 16.9 2.4 18.0 19.4 2.4	2.2 142 2.4 142
412	$E_2 = 2$ E2 = 2	DH43 845.4 37.9		29.0 94.3 30.8 81.8	14.3 1.3	14.8 11.0 6.9	2.0	14.4 16.4 2.4	2.4 142 2.6 140
414	E2 2	DH44 815.7 39.0) 15.4 1.5	18.1 10.3 7.9	1.4	15.4 16.8 2.1	2.5 141
415	E2 2	DH45 735.2 34.4	1.2 618.3	33.6 89.1	14.1 1.5	16.8 9.4 7.8	1.5	15.7 17.2 2.2	2.2 140
416	E2 2	DH46 591.8 37.8		26.6 89.0	17.0 1.5	20.8 11.0 8.1	2.3	15.4 17.7 2.2	2.5 142
417	E2 2	DH47 837.5 32.3		28.9 90.3	14.0 1.4	15.8 9.9 6.9	2.1	14.1 16.2 2.3	2.3 142
418 419	E2 2 E2 2	DH49 642.3 36.3 DH50 740.6 31.3		31.5 81.6 29.8 92.3	15.5 1.5 12.8 1.2	18.6 10.2 7.2 12.5 10.5 6.9	2.2 1.9	14.8 17.0 2.4 14.9 16.8 2.4	2.4 141 2.1 142
420	E2 2 E2 2	DH50 740.0 51.5 DH51 717.5 44.4		25.5 90.0		18.3 11.5 8.0	1.9	16.6 18.2 2.3	2.7 142
421	E2 2	DH52 943.3 35.8			14.4 1.3	14.8 11.2 6.9	1.8	15.1 16.9 2.4	2.4 142
422	E2 2	DH53 914.8 36.1			13.7 1.4	15.2 9.9 6.9	1.8	15.5 17.3 2.5	2.3 141
423	E2 2	DH54 786.2 39.6			19.3 1.5	22.7 12.9 8.2	1.6	15.0 16.6 2.0	2.6 142
424	E2 2	DH55 732.7 37.4		28.0 90.7	14.7 1.4	16.0 10.7 6.5	1.8	14.2 16.0 2.5	2.6 141
425 426	E2 2 E2 2	DH56 665.9 35.8 DH57 783.2 31.7		28.5 85.3 28.8 88.8	11.9 1.3 14.3 1.5	12.4 9.1 7.0 16.7 9.6 6.3	2.1 1.9	15.0 17.1 2.4 15.1 17.0 2.7	2.4 141 2.1 142
420	$E_2 = 2$ E2 = 2	DH58 736.4 35.7			14.3 1.3	16.8 10.2 6.8	2.0	14.0 16.0 2.4	2.1 142 2.5 141
428	E2 2	DH59 837.7 42.0			13.5 1.2	12.6 11.6 6.9	0.8	15.8 16.6 2.4	2.7 140
429	E2 2	DH60 613.1 38.6	1.2 520.9	29.5 81.2	11.8 1.3	11.9 9.4 7.3	2.5	15.0 17.5 2.4	2.6 137
430	E2 2	DH61 649.7 32.0			12.6 1.4	13.8 9.1 7.1	1.9	14.3 16.2 2.3	2.2 142
431	E2 2	DH62 675.4 36.5			15.6 1.3	16.5 11.7 6.5	1.9	13.7 15.6 2.4	2.7 139
432 433	E2 2 E2 2	DH63 762.6 45.7 DH64 903.8 34.4			16.4 1.6 16.0 1.5	20.4 10.5 8.5 18.5 10.9 7.7	1.3 2.3	16.7 18.0 2.1 15.4 17.7 2.3	2.7 141 2.2 142
434	E2 2 E2 2	DH65 884.3 43.6			18.0 1.4	20.1 12.8 8.4	1.8	18.0 19.8 2.4	2.2 142

Table E.1 Continued.

No.	Env.	Rep.	Name	GYLD	GPS	GWI	PS SPSM	TGW	PHT	FLL	FLW	FLA	FLS S	SL	SSN	FSN	TSN S	SC	GSP	HD
435	E2	2	DH66	628.1	38.3	1.3	490.3	32.8	83.8	15.6	1.5	18.7	10.3	8.0	2.0	16.6	18.6 2	2.3	2.3	143
436		2	DH67	574.4	34.3		658.7			14.5			11.8 (1.9		17.0 2		2.3	139
437		2	DH68	473.2	32.5		551.5			16.2			12.0		1.7		16.0 2		2.3	141
438		2	DH69	694.3	42.3		603.2			13.8			10.2		1.3		16.8 2		2.7	140
439		2	DH70	788.9	35.5		795.3			14.9			10.1		2.7		18.9 2		2.2	143
440 441		2 2	DH71 DH72	708.5 610.0	39.0 35.5		628.1 597.4			15.3 14.2		17.1	10.7		1.6 1.9		17.3 2 18.1 2		2.5 2.2	141 143
442		2	DH73	599.3	36.9		594.6			14.2			9.7 [′]		1.9		17.8 2		2.2	143
443		2	DH75	822.2	32.3		871.9			13.1			10.4		2.4		16.1 2		2.4	141
444		2	DH76	693.5	34.0		689.4			14.3			10.1		2.1		16.4 2		2.4	140
445		2	DH77	827.4	32.6		823.3		88.0	18.0	1.3		14.2		2.8		18.7 2		2.0	139
446	E2	2	DH78	798.5	40.4	1.1	696.8	30.4	88.7	14.1	1.3	14.5	10.8	7.8	1.5	16.5	18.0 2	2.3	2.4	139
447		2	DH79	847.6	37.5	1.1	774.8	29.3	96.4	15.2	1.4		11.1 ′		2.1		17.0 2		2.5	142
448		2	DH80	797.6	37.2		723.8			15.2			11.6 '		1.9		17.2 2		2.4	142
449		2	DH81	690.7	35.6		646.7			17.2		23.6			1.1		17.6 2		2.2	141
450		2	DH82	755.0	34.4		885.1			12.6		14.4			2.1		17.1 2		2.3	141
451		2	DH83	733.4	33.3		652.0			13.1			10.4		2.6		15.9 2		2.5	140
452 453		2 2	DH84 DH85	857.6 764.3	35.8 37.1		760.3 683.7			14.4 14.8			11.1 [°] 11.3 [°]		1.6 1.4		15.4 2 16.5 2		2.6 2.5	140 141
454		2	DH85 DH86	852.1	34.1		901.7			15.3			11.2		2.0		17.0 2		2.3	141
455		2	DH87	822.5	43.2		650.7			13.5			10.7		1.0		16.3 2		2.8	138
456		2	DH89	581.9	32.2		548.9			13.1			9.5 (2.0		16.6 2		2.2	141
457		2	DH90	676.0	36.9	1.2	575.8			14.9			11.2 ′		2.5		18.0 2		2.4	139
458	E2	2	DH91	656.0	37.6	1.1	577.0	30.5	89.8	14.8	1.4	15.9	10.9	6.7	2.2	15.1	17.3 2	2.6	2.5	140
459	E2	2	DH92	715.0	34.3	0.9	753.5	26.9	81.9	15.9	1.4		11.8 (1.8	14.8	16.6 2	2.4	2.3	140
460		2	DH93	663.1	44.5		535.7			14.9			11.8 '		1.4		18.1 2		2.6	140
461		2	DH94	795.2	28.4		903.7			12.5			9.4 (2.3		16.9 2		1.9	140
462		2	DH95	958.7	35.3		958.7			16.0			12.0		2.0		17.3 2		2.3	142
463		2	DH96	971.1	29.2		944.6			14.0			10.7		2.6		15.4 2		2.3	141
464 465		2 2	DH97 DH98	831.8 729.1	38.1 44.4		736.7 519.3			15.6 13.6			10.1 ⁷ 10.0 ⁷		1.4 1.0		17.0 2 16.2 2		2.4 2.9	141 138
466		2	DH99		33.8		771.3			16.4			11.2		1.7		16.2 2		2.3	143
467		2	DH100		48.0		544.7			12.5			9.2		1.1		18.0 2		2.8	140
468		2	DH101		41.4		823.5			17.8			11.2		1.4		17.7 2		2.5	141
469	E2	2	DH102	650.9	43.5	1.1	589.1	28.3	88.5	15.4	1.6	19.7	9.6	8.1	1.8	17.0	18.8 2	2.3	2.6	144
470		2	DH103		32.5	1.0	531.5	30.0	77.5	13.0	1.5	15.7	8.5 <i>°</i>	7.2	2.1	15.0	17.1 2	2.4	2.2	145
471		2	DH104		37.7		798.2			15.6			10.9		2.8		18.3 2		2.4	145
472		2	DH105		38.0		618.5			15.5			10.8		1.8		18.0 2		2.3	142
473		2	DH106		42.4		656.3			14.9			10.0		2.1		18.7 2		2.6	141
474 475		2 2	DH107 DH108		32.0 34.7		870.4 689.4			12.4 15.1			10.2 (2.2 2.3		15.9 2 16.9 2		2.3 2.4	139 139
475		2	DH108		30.5		675.6			14.3			10.6		2.5 2.6		17.1 2		2.4	139
477		2	DH110		38.8		554.4			12.2			12.8		1.9		18.0 2		2.4	139
478		2	DH111		39.2		568.5			15.4			11.5		1.9		17.7 2		2.5	141
479		2	DH112		38.7		500.3			13.8			10.0		2.2		18.0 2		2.5	140
480	E2	2	DH113	686.5	35.1	1.1	638.0	30.8	84.6	15.3	1.3	15.7	11.8 (6.5	1.6	14.2	15.8 2	2.5	2.5	140
481		2	DH114		36.5		765.5			14.6			9.9 ′		1.3	15.2	16.5 2	2.3	2.4	141
482		2	DH115				679.3						9.7 ′		2.4		16.5 2		2.2	140
483		2	DH116		30.2		772.8			13.3			9.4		2.4		15.5 2		2.3	141
484		2	DH117		34.1		663.3			13.0		13.9			1.4		15.6 2		2.4	139
485		2	DH119		39.3		608.5			17.3			10.8		2.4		19.1 2		2.3	143
486 487		2 2	DH120 DH121		33.9 35.5		923.0 712.9			16.0 13.4			11.8 [°] 9.3 [°]		2.2 2.8		17.9 2 18.2 2		2.2 2.3	142 141
488		2	DH121 DH122		35.8		641.6			13.4			10.2		2.8 1.6		16.1 2		2.5	141
489		2	DH122 DH123		34.4		602.1			14.1			12.2		2.5		17.4 2		2.3	143
490		2	DH124				722.2			15.3			11.7		1.9		17.0 2		2.3	142
491		2	DH125		31.1		978.7			12.5			9.0		2.7		16.5 2		2.2	141
492		2	DH126				692.7			13.8			9.0		1.4		18.4 2		2.5	144
493		2	DH128				721.8			17.9			13.8 (2.2		17.0 2		2.5	142
494		2	DH129				601.6		86.7				11.0		2.2		16.6 2		2.6	140
495		2	DH130				893.9						10.0		2.5		17.3 2		2.2	141
496	E2	2	DH131	089.8	55.9	1.2	576.2	30.0	89.4	10./	1.8	23.2	9.5	ð.l	3.2	10.5	19.7 2	2.4	2.2	144

Table E.1 Continued.

497 E3 1 DH13 80.1 48.1 5 57.1 30.5 99.7 1.7	No.	Env.	Rep.	Name		GPS	GWPS	SPSM	TGW	PHT	FLL	FLW	FLA	FLS S	L SSN	FSN	TSN SC	GSP	HD
999 E33 1 DHF3 830 441 4 5618 299 903 18319 282.94 71 16 150 166.21 30 129 501 E31 DHF4 4139 13 648 110 171 15 165.23 31 124 173.23 31 124 173.23 31 124 173.23 31 124 173.23 23 112 31 170 173 148 164 165.21 167.23 23 127 114 114 170 173 170 177 15 167.16 167.17 179.99 107 173 129.99 167.17 129.99 167.16 167.17 129.99 167.17 153.18 153.22 22.41 120 138 153.22 133.18 144 144.17 145.14 147.14 147.23 135.33 153.11 154.14 147.14 147.22 153.18 153.14 144.14 147.23																			
500 E3 1 DH6 847.7 47.5 1.5 57.0 2.6 92.7 75.6 2.2 81.0 73.7 1.5 1.6 1.6 6.2 3.0 1.23 502 E3 1 DH7 47.5 35.7 35.0 70.1 1.7 23.4 86.6 3.1 1.4 1.5 1.6 2.2 2.7 1.3 504 E3 1 DH16 65.1 4.3 1.5 1.5 1.5 1.5 1.6 2.1 2.5 1.6 1.2 1.5 1.6 2.1 1.5 1.6 2.2 1.2 1.5 1.6 2.7 1.3 1.5 1.6 2.7 1.3 1.6 1.6 2.7 1.3 1.5 1.6 1.6 1.5 1.5 1.6 1.6 2.9 1.6 1.6 1.6 2.9 1.6 1.6 1.6 1.6 1.6 1.6 1.6 1.6 1.6 1.6 1.6																			
501E31DH7491.5557032.69217.51622.810.7131115.416.23.112502E31DH8614.651.516373.6307103.118.717.71515.217.23.412.7504E31DH9657.143.814454.632.877.11624.512.816.717.215.715.117.116.117.117.116.117.1 </td <td></td>																			
502 E3 1 DH7 491.5 38.6 1.1 42.1 1.7 23.4 9.6 3.1 42.1 2.7 13.4 2.7 13.4 2.7 13.4 2.7 13.4 2.7 13.4 2.7 13.4 2.7 13.6 3.1 15.1 15.5 15.1 15.2 16.2 2.7 13.0 3.1 15.1 15.5 17.6 2.4 13.2 8.6 1.4 15.5 16.2 2.9 12.5 15.6 2.2 12.5 15.6 2.2 2.1 12.7 13.0 11.6 13.8 13.4 3.4 13.9 2.0 17.7 17.1 17.1 17.1 17.1 17.1 17.1 17.1 17.1 13.1 13.1 13.3 15.5 17.7 13.9 17.1 17.1 17.1 17.1 17.1 17.1 17.1 17.1 17.1 17.1 17.1 17.1 17.1 17.1 17.1 17.1 17.1 17.1 13.1 17.1 13.1 17.1 17.1 17.1 13.1 17.1 17.1																			
504 E33 1 DH9 655.1 43.8 14 454.6 32.8 97.4 20.0 19 29.9 10.7 12 14 16.8 2.3 12 125 506 E31 DH112 582.1 42.5 18.7 16.7 12.9 96 10.5 14.1 15.8 12.5 16.7 12.9 96 10.7 12.5 18.1 2.6 2.6 130 508 E31 DH115 74.6 37.8 13.0 95.1 15.5 17.3 10.7 18 18.8 15.8 2.7 130 511 E31 DH117 64.7 37.7 31.9 17.1 14.8 13.3 12.2 12.7 11.0 18.1 16.8 13.3 12.2 12.2 11.0 11.8 16.8 13.3 12.2 12.2 12.2 12.5 13.3 14.8 13.3 12.6 13.3 12.6 13.3 14.1 15.1	502	E3	1	DH7	491.5	38.6	1.2											2.7	133
505 E3 1 DH12 S21 425 145 197 16 243 128.86 14 155 169 20 32 125 506 E3 1 DH13 548.3 47.8 14 887.4 939 200.17 72.2 16.7 12 15 18.8 15.6 22 29 12 508 E3 1 DH14 76.6 37.5 33.0 951 15.1 12.7 12.5 18.8 15.2 2.2 12 12 510 E3 1 DH14 70.0 42.5 15.3 33.0 951 15.4 12.7 11.0 18.1 15.3 18.2 2.2 12.4 13.1 14.1 14.3 13.1 14.1 14.3 13.3 14.3 13.3 14.3 13.3 14.3 12.2 2.2 12.5 15.1 15.1 16.0 12.2 12.2 13.1 14.1 13.3 <t< td=""><td></td><td></td><td>1</td><td>DH8</td><td>614.6</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td>15.2</td><td>$16.7 \ 2.2$</td><td>3.4</td><td></td></t<>			1	DH8	614.6											15.2	$16.7 \ 2.2$	3.4	
506E31DH12S82.142514400832.587.0167.1722.996.701514.1156.2229.128507E31DH14475.638.81.3363.622.195.916.61620.910.770.32153.18.52.72.1129509E31DH1683.442.11.5577.333.095.1155.1.720.593.691.51.818.52.22.412511E31DH1860.842.71.443.131.444.182.322.661.51.31.8.22.4132.4135513E31DH1860.830.71.649.630.11.91.41.01.51.61.31.4.22.82.61.51.31.8.42.32.81.0516E3DH1260.03.681.351.23.01.01.4.21.61.51.61.61.51.51.61.62.61.71.61.62.61.61.61.61.61.61.61.61.71.71.91.61.62.61.71.61.61.51.81.62.22.61.51.61.81.62.71.61.61.61.71.61.61.61.71.71.61.61.61.71.7 <td></td>																			
507 E33 1 DH14 387.4 93.9 200.17 27.2 11.6 7.1 22 15.3 18.3 2.6 2.1 201 508 E31 DH16 87.6 33.1 95.9 16.6 1.0 10.0 1.3 18.8 15.6 2.2 1.4 510 E31 DH16 87.6 3.8 1.5 1.7 2.5 3.6 3.5 3.6 1.5 1.8 1.6 2.2 1.1 1.8 1.5 1.5 1.8 1.6 1.7 1.4 1.8 1.6 1.2 1.2 1.3 1.8 1.5 2.2 1.1 1.6 1.5 1.3 1.8 2.2 1.2 1.3 1.8 1.5 2.2 1.2 1.3 1.8 1.5 2.2 1.2 1.5 1.5 1.3 1.4 1.6 2.2 1.2 1.6 1.1 1.6 1.4 1.6 1.2 1.6 1.1 1.6 <td></td>																			
508 E3 1 DH14 475.6 388 1.3 365.6 32.1 95.9 16.6 10.7 0.0 18 18.8 18.5 2.2 2.4 12.2 510 E3 1 DH16 83.4 42.1 1.5 57.5 30.0 95.1 15.5 1.7 20.5 93.6 9.1 1.8 1.8 1.6 2.2 2.4 1.2 513 E3 1 DH118 60.8 82.7 1.4 43.1 94.4 1.8 2.3 1.8 1.5 1.6 1.8 1.2 2.6 1.4 1.8 1.3 1.4 2.5 1.5 1.6 1.8 1.4 1.6 2.4 1.8 1.8 1.5 1.6 1.8 1.4 1.6 2.2 1.6 1.8 1.8 1.5 2.2 1.6 1.6 2.8 1.7 1.1 1.6 2.2 1.2 1.1 1.5 1.6 1.8 1.8																			
500 E3 1 DH15 774.6 375.7 31.0 91.0 14.8 1.5 17.3 10.0 1.1 13.8 15.6 2.2 2.4 12.4 511 E3 1 DH17 700.0 42.5 1.5 516.3 32.7 94.9 17.8 1.6 22.7 11.0 7.4 1.8 1.43 16.1 2.2 2.6 1.2 511 E3 1 DH19 49.2 1.4 1.43 1.7 4.4 2.3 1.6 2.3 1.1 0.6 8.1 2.2 2.8 1.2 515 E3 1 DH12 8.3 1.6 1.2 2.1 1.3 1.6 2.2 1.2 1.6 1.8 2.2 9.0 7.8 2.5 1.6 1.8 2.2 9.1 1.5 1.6 1.8 2.2 1.3 1.6 1.2 2.2 1.2 1.1 1.5 1.6 1.2 1.2																			
511 E33 1 DH17 790.0 42.5 1.5 516.3 32.7 98.9 17.8 1.6 22.7 11.0 74 1.4 13.1 14 44.8 12.2 33.5 83.7 5.1 9 15.6 1.3 11.4 10.2 2.6 1.8 23.3 2.6 1.5 13.3 14.8 2.3 2.8 13.7 515 E3 1 DH20 80.8 3.7 14.2 16.1 1.8 2.29 9.0 7.8 2.0 1.6 1.8 1.29 9.0 7.8 2.0 1.6 1.6 2.2 1.2 1.3 1.6 2.2 1.2 1.3 1.6 2.2 1.2 1.3 1.6 2.2 1.6 1.8 1.1 1.6 2.4 2.6 1.2 1.1 1.5 1.6 1.8 1.7 1.6 1.8 1.7 1.6 1.8 1.7 1.6 1.8 1.7 1.6 1.6 1.6 1.6 1.6 1.6 1.6 1.6 1.6 1.6 1.6																			
512 E3 1 DH18 605.8 427 1.4 435.1 31.4 94.4 18,7 22.3 35.8 3.7 5.19 1.6 175 2.3 2.4 135 513 E3 1 DH20 808.3 50.7 1.6 495.6 30.1 91.5 20.4 1.9 31.4 10.5 7.8 1.0 1.3 1.65 2.4 1.3 1.6 2.2 2.3 1.0 2.1.8 1.6 2.3 1.7 1.4 1.61 2.2 1.2 1.7 1.6 2.2 1.2 1.8 1.5 1.6 1.8 2.2 1.3 1.6 2.2 1.2 1.8 1.5 1.4 1.6 2.2 2.2 1.2 1.8 1.5 1.4 1.6 2.2 2.2 1.2 1.8 1.6 1.4 1.6 2.2 2.2 1.2 1.5 1.5 1.6 1.8 1.6 1.6 1.8 1.6 1.6 1.6 1.6 1.6 1.6 1.6 1.6 1.6 1.2 1.6	510	E3	1	DH16	834.4	42.1	1.5	573.5	33.0	95.1	15.5	1.7	20.5	9.3 6	9 1.5	13.8	15.3 2.2	2.8	124
513 E3 1 DH19 4692 14 33 734 64 952 164 18 233 92 66 181 233 22 18 13 142 23 14 165 18 15 163 181 233 22 233 1052 189 16 237 119 68 31 134 165 24 22 131 516 E3 1 DH22 852.4 17 17 4913 327 114.2 161 18 22.9 90 78 67 15 14.1 156 2.2 12.5 12 14.1 15.2 22.1 25.5 15 13.1 14.1 16.2 23.2 12.1 13.1 14.1 16.2 23.2 12.1 15.3 13.3 10.6 10.3 10.2 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 10.1 11.1 11.1 11.1 11.1 10.1 10.1 10.1 10.1 10.1 10.1																			
514 E3 1 DH20 8083 507 1.6 495 30.1 91.5 20.4 1.9 31.4 10.5 71.9 6.8 3.1 13.4 16.5 2.4 2.2 131 516 E3 1 DH22 82.4 51.7 1.7 491.3 32.7 114.2 16.1 8 2.9 0.6 1.5 1.1 1.6 2.2 2.2 1.5 1.5 1.4 1.6 2.2 2.2 1.5 1.1 1.6 2.2 2.2 1.5 1.1 1.6 2.2 2.2 1.0 1.5 1.4 1.6 2.2 2.2 1.5 1.1 1.6 2.2 2.2 1.2 5.6 1.1 1.6 2.2 2.2 1.0 1.6 1.6 2.1 1.6																			
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544E31DH51632.750.01.5434.229.998.620.31.828.811.47.91.415.917.32.22.9131545E31DH52698.248.01.5476.929.587.915.41.720.79.27.20.815.516.32.32.9127546E31DH53768.846.11.6491.631.083.618.71.827.010.37.20.915.216.12.22.9129547E31DH54858.650.51.9456.434.994.418.11.926.89.78.01.814.616.42.13.1123548E31DH55875.140.51.2707.428.5101.316.31.620.210.46.32.414.416.82.72.4129549E31DH56848.532.91.2691.0100.413.81.516.19.45.92.311.914.22.42.3125550E31DH57874.642.21.4638.830.698.314.31.719.78.26.32.217.42.82.4129551E31DH58689.147.61.5475.331.1101.315.515.818.3	542	E3	1	DH49	682.3	55.8	1.8	384.9	31.7	97.5	19.7	1.8						3.2	130
545E31DH52698.248.01.5476.929.587.915.41.720.79.27.20.815.516.32.32.9127546E31DH53768.846.11.6491.631.083.618.71.827.010.37.20.915.216.12.22.9129547E31DH54858.650.51.9456.434.994.418.11.926.89.78.01.814.616.42.13.1123548E31DH55875.140.51.2707.428.5101.316.31.620.210.46.32.414.416.82.72.4129549E31DH56848.532.91.2691.0100.413.81.516.19.45.92.311.914.22.42.3125550E31DH57874.642.21.4638.830.698.314.31.719.78.26.32.217.42.82.4129551E31DH58689.147.61.5475.331.1101.315.515.318.310.56.91.514.215.72.33.0127552E31DH6080.154.31.7519.831.395.718.91.726.2<	543	E3	1	DH50	904.9	33.6	1.3	671.8	35.1	100.8	14.3	1.5	17.1	9.5 6	5 2.4	13.4	$15.8\ 2.4$	2.1	125
546 E3 1 DH53 768.8 46.1 1.6 491.6 31.0 83.6 18.7 1.8 27.0 10.3 7.2 0.9 15.2 16.1 2.2 2.9 129 547 E3 1 DH54 858.6 50.5 1.9 456.4 34.9 94.4 18.1 1.9 26.8 9.7 8.0 1.8 14.6 16.4 2.1 3.1 123 548 E3 1 DH55 875.1 40.5 1.2 707.4 28.5 101.3 16.3 1.6 20.2 10.4 6.3 2.4 14.4 16.8 2.7 2.4 129 549 E3 1 DH56 848.5 32.9 1.2 691.0 100.4 13.8 1.5 16.1 9.4 5.9 2.3 11.9 14.2 2.4 2.3 125 550 E3 1 DH57 874.6 42.2 1.4 638.8 30.6 98.3 14.3 1.7 19.7 8.2 6.3 2.2 15.2																			
547 E3 1 DH54 858.6 50.5 1.9 456.4 34.9 94.4 18.1 1.9 26.8 9.7 8.0 1.8 14.6 16.4 2.1 3.1 123 548 E3 1 DH55 875.1 40.5 1.2 707.4 28.5 101.3 16.3 1.6 20.2 10.4 6.3 2.4 14.4 16.8 2.7 2.4 129 549 E3 1 DH56 848.5 32.9 1.2 691.0 100.4 13.8 1.5 16.1 9.4 5.9 2.3 11.9 14.2 2.4 2.3 125 550 E3 1 DH57 874.6 42.2 1.4 638.8 30.6 98.3 14.3 1.7 19.7 8.2 6.3 2.2 15.2 17.4 2.8 2.4 129 551 E3 1 DH59 1071.2 36.6 1.1 951.3 30.6 100.9 14.8 1.6 19.0 9.2 6.5 1.4 13.3																			
548 E3 1 DH55 875.1 40.5 1.2 707.4 28.5 101.3 16.3 1.6 20.2 10.4 6.3 2.4 14.4 16.8 2.7 2.4 129 549 E3 1 DH56 848.5 32.9 1.2 691.0 100.4 13.8 1.5 16.1 9.4 5.9 2.3 11.9 14.2 2.4 2.3 125 550 E3 1 DH57 874.6 42.2 1.4 638.8 30.6 98.3 14.3 1.7 19.7 8.2 6.3 2.2 15.2 17.4 2.8 2.4 129 551 E3 1 DH58 689.1 47.6 1.5 475.3 31.1 101.3 15.5 18.3 10.5 6.9 1.5 14.2 15.7 2.3 3.0 127 552 E3 1 DH69 1071.2 36.6 1.1 951.3 30.6 100.9 14.8 1.6 19.0 9.2 6.5 1.4 13.3 14.7 <td></td>																			
549E31DH56848.532.91.2691.0100.413.81.516.19.45.92.311.914.22.42.3125550E31DH57874.642.21.4638.830.698.314.31.719.78.26.32.215.217.42.82.4129551E31DH58689.147.61.5475.331.1101.315.51.518.310.56.91.514.215.72.33.0127552E31DH591071.236.61.1951.330.6100.914.81.619.09.26.51.413.314.72.32.5122553E31DH60880.154.31.7519.831.395.718.91.726.210.98.01.416.517.92.23.0126554E31DH61642.137.31.1564.231.793.017.31.824.29.77.22.014.616.62.32.3131555E31DH62771.752.61.7462.7103.119.51.726.311.47.20.415.515.92.23.3126556E31DH63666.055.42.0331.333.693.516.81.824.3 <td></td>																			
550 E3 1 DH57 874.6 42.2 1.4 638.8 30.6 98.3 14.3 1.7 19.7 8.2 6.3 2.2 15.2 17.4 2.8 2.4 129 551 E3 1 DH58 689.1 47.6 1.5 475.3 31.1 101.3 15.5 1.5 18.3 10.5 6.9 1.5 14.2 15.7 2.3 3.0 127 552 E3 1 DH59 1071.2 36.6 1.1 951.3 30.6 100.9 14.8 1.6 19.0 9.2 6.5 1.4 13.3 14.7 2.3 2.5 122 553 E3 1 DH60 880.1 54.3 1.7 519.8 31.3 95.7 18.9 1.7 26.2 10.9 8.0 1.4 16.5 17.9 2.2 3.0 126 554 E3 1 DH61 642.1 37.3 1.1 564.2 31.7 93.0 17.3 1.8 24.2 9.7 7.2 2.0																			
551E31DH58689.147.61.5475.331.1101.315.51.518.310.56.91.514.215.72.33.0127552E31DH591071.236.61.1951.330.6100.914.81.619.09.26.51.413.314.72.32.5122553E31DH60880.154.31.7519.831.395.718.91.726.210.98.01.416.517.92.23.0126554E31DH61642.137.31.1564.231.793.017.31.824.29.77.22.014.616.62.32.3131555E31DH62771.752.61.7462.7103.119.51.726.311.47.20.415.515.92.23.3126556E31DH63666.055.42.0331.333.693.516.81.824.39.28.50.915.816.72.03.3123557E31DH64830.242.61.6515.736.1111.816.21.620.310.27.51.614.716.32.22.6123																			
553E31DH60880.154.31.7519.831.395.718.91.726.210.98.01.416.517.92.23.0126554E31DH61642.137.31.1564.231.793.017.31.824.29.77.22.014.616.62.32.3131555E31DH62771.752.61.7462.7103.119.51.726.311.47.20.415.515.92.23.3126556E31DH63666.055.42.0331.333.693.516.81.824.39.28.50.915.816.72.03.3123557E31DH64830.242.61.6515.736.1111.816.21.620.310.27.51.614.716.32.22.6123				DH58	689.1	47.6	1.5		31.1	101.3	15.5	1.5	18.3	10.5 6	9 1.5	14.2	$15.7\ 2.3$		
554 E3 1 DH61 642.1 37.3 1.1 564.2 31.7 93.0 17.3 1.8 24.2 9.7 7.2 2.0 14.6 16.6 2.3 2.3 131 555 E3 1 DH62 771.7 52.6 1.7 462.7 . 103.1 19.5 1.7 26.3 11.4 7.2 0.4 15.5 15.9 2.2 3.3 126 556 E3 1 DH63 666.0 55.4 2.0 331.3 33.6 93.5 16.8 1.8 24.3 9.2 8.5 0.9 15.8 16.7 2.0 3.3 123 557 E3 1 DH64 830.2 42.6 1.6 515.7 36.1 111.8 16.2 1.6 20.3 10.2 7.5 1.6 14.7 16.3 2.2 2.6 123 557 E3 1 DH64 830.2 42.6 1.6 515.7 36.1 111.8 16.2 1.6 20.3 10.2 7.5 1.6																			
555 E3 1 DH62 771.7 52.6 1.7 462.7 . 103.1 19.5 1.7 26.3 11.4 7.2 0.4 15.5 15.9 2.2 3.3 126 556 E3 1 DH63 666.0 55.4 2.0 331.3 33.6 93.5 16.8 1.8 24.3 9.2 8.5 0.9 15.8 16.7 2.0 3.3 123 557 E3 1 DH64 830.2 42.6 1.6 515.7 36.1 111.8 16.2 1.6 20.3 10.2 7.5 1.6 14.7 16.3 2.2 2.6 123																			
556 E3 1 DH63 666.0 55.4 2.0 331.3 33.6 93.5 16.8 1.8 24.3 9.2 8.5 0.9 15.8 16.7 2.0 3.3 123 557 E3 1 DH64 830.2 42.6 1.6 515.7 36.1 111.8 16.2 1.6 20.3 10.2 7.5 1.6 14.7 16.3 2.2 2.6 123																			
557 E3 1 DH64 830.2 42.6 1.6 515.7 36.1 111.8 16.2 1.6 20.3 10.2 7.5 1.6 14.7 16.3 2.2 2.6 123																			
558 E3 1 DH65 721.8 55.6 1.7 420.4 31.0 91.1 18.8 1.6 23.4 12.0 8.0 0.9 17.0 17.9 2.2 3.1 125	558	E3	1															3.1	125

Table E.1 Continued.

No.	Env.	Rep.	Name	GYLD	GPS	GWPS	SPSM	TGW	PHT	FLL	FLW	FLA	FLS	SL	SSN	FSN	TSN	SC	GSP	HD
559	E3	1	DH66	652.4		1.5	421.7	34.8	105.2		2.1	30.4		8.1	3.7		20.8	2.6	2.1	132
560	E3	1	DH67	845.4		1.5	573.6		97.4				10.6		1.1		17.0	2.4	2.7	125
561 562	E3 E3	1 1	DH68 DH69	609.3 946.3		1.2 1.5	503.1 612.1	27.4 33.0	97.0 98.4		1.8 1.7	25.8 21.0		7.4 6.9	1.0 0.9		16.3 15.3	2.2 2.2		127 124
563	E3	1	DH70	661.2		1.3	490.2	31.7	98.6		1.7	23.8		8.0	1.8	14.4		2.2		132
564	E3	1	DH71	826.0		1.5	555.1	31.2	99.8		1.9		10.3				18.6			130
565	E3	1	DH72	835.7	41.7	1.4	617.7	31.8	98.1		1.7	18.6		6.9	2.8		18.0		2.3	129
566	E3	1	DH73	804.7		1.6	506.4	30.4	99.6	16.2	1.7	22.2	9.4	7.8	1.3	15.9	17.2	2.2	2.9	130
567	E3	1	DH75	941.7		1.3	723.8		103.5		1.8	24.6		6.9	1.9		15.4	2.2		122
568	E3	1	DH76	916.5		1.1			91.3			22.7					15.6			130
569 570	E3 E3	1 1	DH77 DH78	746.8 862.2		1.3 1.6	581.2 530.9		105.3 92.0		1.6 1.6	22.3 21.0				15.8	18.4 16.3	2.4		127 125
571	E3	1	DH79	670.1		1.0	399.1		101.2			19.1					16.5			125
572	E3	1	DH80	742.3		1.5	480.8		101.2			24.6					17.0			120
573	E3	1	DH81	719.8		1.2	584.8		101.0			19.5		6.1			17.0			127
574	E3	1	DH82	793.8	51.3	1.8	436.9	32.2	100.1	15.0	1.6	19.2	9.3	8.1	0.6	16.2	16.8	2.1	3.1	122
575	E3	1	DH83	828.1		1.4	584.0		110.5			23.2			2.6	14.2		2.3		126
576	E3	1	DH84	1017.3		1.3			102.4			18.2						2.0		122
577	E3	1	DH85	921.5		1.2	792.1		90.6				10.2		2.1		15.1	2.4		128
578 579	E3 E3	1 1	DH86 DH87	787.1 893.4		1.4 1.4	571.2 642.3		104.8 101.3		1.6 1.7		11.1 10.7		1.8 1.0		16.3 15.8	2.7		128 121
580	E3	1	DH89	804.8		1.4	591.8	33.5	99.8		1.7		10.7		2.2			2.3		121
581	E3	1	DH90	768.8		1.3	580.2		91.2			19.8					15.7			125
582	E3	1	DH91	714.4	42.8	1.4	498.9	31.7	109.0	17.0	1.5	20.5	11.1	7.1	1.9	14.6	16.5	2.4	2.6	125
583	E3	1	DH92	898.9		1.3	708.3	32.9	97.5	16.8	1.7		10.3	6.8	1.9	13.4	15.3	2.2		126
584	E3	1	DH93	888.8		1.7	523.8		87.8		1.8	23.2		7.8			16.9	2.2		126
585	E3	1	DH94	838.3		1.2	691.1		103.2			19.1					16.8			130
586 587	E3 E3	1 1	DH95 DH96	1026.1 759.0		1.3 1.3	799.1 564.3	36.0	102.0 105.1			18.0 19.6					16.0 14.9	2.1		121 128
588	E3 E3	1	DH96 DH97	884.6		1.5	581.2	34.2	105.1		1.0	23.8		0.4 7.3			14.9			128
589	E3	1	DH98	712.6		1.8	404.2		91.5			20.6		7.8				2.0		120
590	E3	1	DH99	722.2		1.6	466.0	32.0	91.5			27.7		7.0	1.5		17.9			130
591	E3	1	DH100	877.3	47.9	1.4	620.9	30.5	80.5	14.6	1.7	19.7	8.6	6.9	1.5	15.3	16.8	2.4	2.8	125
592	E3	1	DH101			1.4	626.5	•	99.4		1.8	24.9		7.5	1.7		17.2			126
593	E3	1		669.8		1.4	462.2	29.2	99.7		1.8		11.7		1.9		18.8	2.3		131
594 595	E3 E3	1 1	DH103	470.3		1.4 1.3	342.8 551.0	30.7	92.4 104.0		2.0 1.7	30.2	9.3 11.9	7.2	1.9	14./ 14.6	16.6	2.3 2.4		132 132
595	E3	1		760.8		1.5	541.9	29.0	97.1		1.7		11.9		1.7		16.3	2.4		126
597	E3	1		873.8		1.5	592.4	31.1	99.6		1.8	22.7		7.6	2.0		18.3	2.4		128
598	E3	1		726.8		1.1	642.6	31.4	98.0		1.8	22.2		6.7			14.7			125
599	E3	1	DH108	488.1	40.1	1.3	367.2	30.5	106.8	17.4	1.6	22.7	10.6	6.4	2.4	14.7	17.1	2.7	2.3	125
600	E3	1		634.5		1.3	485.1		92.0			23.0					16.6			129
601	E3	1		545.4		1.4	391.8		109.2			19.3			2.1	16.0		2.3		127
602 603	E3 E3	1 1		517.6 608.4		1.1 1.3	452.5 458.8		103.7 90.2		1.6 1.6	24.4 20.4		6.8 7.2	2.1 2.5		15.8 17.7	2.3 2.5		127 128
604	E3	1		776.2		1.3	438.8 593.9		106.4			20.4				13.2		2.5		128
605	E3	1		622.4		1.3	492.0	31.7	78.4		1.7	23.7		7.3		14.4		2.1	2.7	128
606	E3	1	DH115			1.1	494.8	30.9	103.9	15.9	1.6	20.5	9.8					2.3	2.3	127
607	E3	1	DH116	780.0	30.9	1.1	740.0								3.0	12.4	15.4	2.4	2.0	123
608	E3	1	DH117			1.3	619.9										15.8			124
609	E3	1	DH119			1.5	475.1										17.5			128
610	E3	1		941.8		1.2	812.6										17.3 16.5			130
611 612	E3 E3	1 1		737.3 635.9		1.3 1.6	547.4 386.8										16.5			131 131
613	E3	1	DH122 DH123			1.5	379.6										16.1			128
614	E3	1		744.5		1.3	558.5										17.9		2.3	
615	E3	1		789.9		1.4	577.0	33.2	89.8	15.7	1.8	22.0	8.9	6.5			15.4			128
616	E3	1	DH126			1.6	506.2										18.0		2.8	130
617	E3	1		567.3		1.1	510.1										17.2			131
618	E3	1		888.1		1.6	550.9										16.2			127
619 620	E3 E3	1 1		698.6 659.9		1.2 1.3	565.7 520.1										16.3			128 134
020	1.3	1	ונוווע	039.9	50.4	1.3	520.1	55.2	10/.1	1/.4	1.7	∠0.4	9.1	1.1	5.9	13.0	17./	∠.0	1.9	134

Table E.1 Continued.

No.	Env.	Rep.	Name	GYLD	GPS	GWPS	SPSM	TGW	PHT	FLL	FLW	FLA	FLS	SL	SSN	FSN	TSN	SC	GSP	HD
621	E3	2	DH1	854.9		1.4	590.4	30.8	99.1		1.5	16.2		6.5	0.6		15.4	2.4	3.1	124
622	E3	2	DH3	508.4		1.2			106.5					6.3	1.9		15.6	2.5	2.7	
623	E3	2	DH4	763.1		1.3	607.5	31.8	90.5		1.7	22.4		6.6	1.9	14.9		2.5	2.8	129
624 625	E3 E3	2 2	DH5 DH6	758.5 818.4	40.8	1.2 1.6	628.4 500.2	31.2 32.1	92.6 99.1		1.7 1.6	23.0 20.7		7.6	1.7 0.8	15.0	16.7 16.4	2.2 2.2		130 122
626	E3	2	DH7	780.7		1.0	643.1	31.3	87.9		1.8	25.1			3.1			2.2		132
627	E3	2	DH8	731.5		1.4	535.9		101.8		1.5	21.6		7.2	1.8	14.7		2.3		127
628	E3	2	DH9	382.1		1.7	222.9	34.0	95.6		1.8	25.6			2.1		20.1			131
629	E3	2	DH11	548.8	48.1	1.8	310.2	36.1	113.3	19.4	1.5	23.6	12.6	8.6	1.6	15.5	17.1	2.0	3.1	127
630	E3	2	DH12			1.5	413.0	32.5	87.8		2.0	28.8		7.0	1.1		16.3			128
631	E3	2	DH13		53.1	1.5	437.2	28.4	97.2		1.7	25.0		7.4	1.9	17.1		2.6		129
632	E3	2	DH14			1.4	446.7	33.4	93.5		1.7	24.9				14.9		2.4		129
633 634	E3 E3	2 2	DH15 DH16		38.6	1.3	668.1 307.1	33.1 32.7	96.3 94.7		1.6 1.7	18.2 22.4		7.3 6.8		14.6 13.9				122 125
635	E3 E3	2	DH10 DH17	478.3		1.6 1.7	410.5		100.3			22.4		0.8 8.1	1.1 1.1	15.9		2.2		125
636	E3	2	DH18	438.9		1.7	342.0	55.2	96.7		2.2	32.6		7.8	1.3		18.0			136
637	E3	2	DH19	788.0		1.5	527.8	34.1	106.5			21.6		6.5		13.1		2.2		127
638	E3	2	DH20	579.4	44.4	1.3	434.0	29.7			1.8	29.1	11.5	6.9		14.5		2.3	3.1	131
639	E3	2	DH21	777.6	40.3	1.3	577.7	32.7	104.1	19.5	1.7	25.8	11.7	7.2	1.9	13.9	15.8	2.2	2.9	129
640	E3	2	DH22	646.4	51.1	1.6	396.8	33.3	115.2	17.9	1.9	27.1		7.5	1.7	16.3		2.4	3.1	129
641	E3	2	DH23	855.6		1.3	654.6		104.1		1.7	23.4				12.7				124
642	E3	2	DH24	603.8	40.5	1.3	452.9		101.7		1.6	20.2				14.8		2.2		122
643 644	E3 E3	2	DH25 DH26	744.2 813.8		1.3 1.3	573.8		97.3 85.1			23.4			1.8 1.3		17.1	2.4 2.3		126 129
644 645	E3 E3	2 2	DH20 DH27	754.6		1.5	617.9 581.8	31.8	105.3		1.7 1.7	23.7 27.3			1.5	14.2 14.0		2.5 2.4		129
646	E3	2	DH27 DH28	714.5		1.3	503.5		105.5		1.7	27.5				14.0		2.4		129
647	E3	2	DH29			1.8	496.4	32.1	82.3			20.8		8.1	1.3		17.5			128
648	E3	2	DH30			1.6	360.4	34.1	98.6		1.8	27.0				15.3		2.3		128
649	E3	2	DH31	809.0	42.2	1.3	623.2	30.6	97.4	17.2	1.7	23.2	10.1	7.5	1.9	15.2	17.1	2.3	2.8	131
650	E3	2	DH32	597.0	39.3	1.1	542.2		91.9		1.7	20.3		6.9	1.7	14.9	16.6	2.4	2.6	134
651	E3	2	DH33	510.1		1.4	354.0		99.3		1.9	29.0		7.2		16.5				136
652	E3	2	DH34			1.7	490.8		105.2		1.8	27.6			1.1		17.3			125
653 654	E3 E3	2 2	DH35			1.3 1.5	476.7 502.7	33.4 32.0	101.2 93.3		1.9 1.9	25.8 27.8		7.2	1.9 1.3	14.1 16.3		2.2 2.1		128 130
655	E3 E3	2	DH36 DH37	484.1	45.4 50.4	1.5	320.6	32.0 31.7	93.5 98.6		1.9	27.8			1.5	15.8		2.1		128
656	E3	2	DH38	750.2		1.6	483.4		90.7		1.8	25.1				14.7				120
657	E3	2	DH39	765.8		1.3	592.3	31.3	104.0		1.7	21.0		6.0	1.8	13.8		2.6		128
658	E3	2	DH40	419.3	40.9	1.3	318.6	32.8	111.6	17.7	1.6	21.8	11.7	7.6	0.8	15.7	16.5	2.2	2.6	126
659	E3	2	DH41	861.3	41.2	1.3	671.3	31.8	99.6	17.4	1.7	22.8			1.5	14.5	16.0	2.3	2.8	130
660	E3	2	DH42			1.5	574.4		102.8		1.5	20.7			1.8	15.8				129
661	E3	2	DH43	673.8		1.4	471.9	32.1	98.8		1.6	22.6		7.0		14.4		2.4		129
662	E3	2	DH44			1.4	395.8		104.4		1.7	27.6				14.4				131 127
663 664	E3 E3	2 2	DH45 DH46	578.9 592.5	36.9	1.4 1.4	410.9 430.9	35.5 32.4	96.9 99.4		1.7 1.9	20.6 31.0		7.1	2.0 1.7	14.4	16.4	2.3		127
665	E3	2	DH40 DH47	649.0	45.0	1.4	478.3	33.7	90.4		1.9	22.7			1.7	15.4		2.1		130
666	E3	2	DH49			1.4	420.1	32.9	98.2		1.7					14.8		2.2	3.1	131
667	E3	2	DH50			1.6	411.9		108.0			19.5				13.8		2.2		125
668	E3	2		649.8		1.3			98.5										2.8	130
669	E3	2		847.6		1.4	621.9		88.4					7.0		14.4			3.2	128
670	E3	2		882.1		1.3	670.8		85.1			23.9		6.7		14.5				130
671	E3	2		720.2		1.7			100.4							14.5				124
672	E3	2		926.0		1.2			105.6 101.4			20.2 16.8				14.3				127
673 674	E3 E3	2 2	DH56 DH57	984.3 788.3		1.2 1.3			101.4 95.8			10.8				13.0 14.0				125 128
675	E3	2		880.2					101.2			19.0				14.0				126
676	E3	2		932.2					95.5			19.6				13.3				123
677	E3	2		809.4		1.6	518.2		102.0							14.6				127
678	E3	2	DH61	502.1	37.4	1.2			90.8	17.0	1.5	20.5	11.4	7.3		14.5			2.6	130
679	E3	2		746.0		1.2			93.5							12.9				127
680	E3	2		833.0		1.8			91.0							15.5				124
681 682	E3	2		923.7					109.5			22.3 22.3				14.9				126
682	E3	2	DH65	808.8	38.2	1.8	444.0	30.7	99.0	1/./	1.0	22.3	11.1	0.2	0.4	17.0	17.4	2.1	3.4	124

Table E.1 Continued.

No.	Env.	Rep.	Name	GYLD	GPS	GWPS	SPSM	TGW	PHT	FLL	FLW	FLA	FLS SI	_ SSN	FSN	TSN SC	GSP	HD
683	E3	2	DH66	510.4	42.2		355.2		102.0			35.1				17.9 2.3	2.7	133
684	E3	2	DH67	818.6	40.5		568.5			17.9			10.8 6.			16.7 2.5	2.7	126
685	E3	2	DH68	570.4	38.9		460.4		93.1	18.7			11.1 7.			16.0 2.3	2.8	127
686 687	E3 E3	2 2	DH69 DH70	820.1 687.0	41.5 43.1		578.4 607.9		93.5 99.8	15.9 17.2			10.0 6. 9.9 7.			14.3 2.3 17.8 2.4	3.1 2.7	125 131
688	E3	2	DH71	481.2	47.1		331.0		93.3	20.2			10.9 7.			16.3 2.2	3.1	131
689	E3	2	DH72	824.6	43.9		569.8		96.9	15.7		21.7				17.7 2.4	2.7	130
690	E3	2		692.3	40.4		529.7		94.9	16.8			9.4 6.			16.4 2.5	2.8	130
691	E3	2	DH75	877.8	37.0	1.3	685.7		96.7	15.5			8.1 6.			15.3 2.2	2.7	121
692	E3	2	DH76	983.3	34.0	1.1	873.3		92.7	17.3	1.7	22.5	10.5 6.4	4 2.0	12.8	14.8 2.3	2.6	129
693	E3	2	DH77	550.0	40.8	1.3	426.3		102.9				15.8 7.		15.0	16.7 2.3	2.7	127
694	E3	2		895.1	52.2		503.1	35.5	102.6				10.4 7.			17.0 2.2	3.2	124
695	E3	2	DH79	974.9	46.5		620.5	•	104.5				11.0 7.			16.1 2.3	3.2	126
696	E3	2	DH80	748.9	51.7		458.1		100.4				12.0 7.			17.1 2.4	3.2	130
697 698	E3 E3	2 2	DH81 DH82	593.1 705.3	41.4 41.9		454.5 491.5		90.2 101.1				9.9 6.			15.2 2.4 15.2 2.1	2.9 3.0	128 125
698 699	E3 E3	2	DH82 DH83	703.5 847.2			516.3		95.0				9.4 7.4 11.4 7.4			16.3 2.2	3.0 3.2	123
700	E3	2	DH84	1031.6			752.4			13.8			10.1 7.			14.5 2.0	2.8	122
701	E3	2	DH85	841.7	35.1		695.6		91.8				10.7 6.			14.6 2.3	2.7	129
702	E3	2	DH86	795.7	42.4		556.0		100.4				11.9 6.			15.4 2.5	3.0	125
703	E3	2	DH87	993.9	52.8	1.5	648.3	29.4	97.6	16.8	1.5	20.1	11.1 7.4	4 0.1	15.9	16.0 2.2	3.3	122
704	E3	2	DH89	751.7	35.4	1.2	615.7	33.1	102.6	17.1	1.7	22.8	10.2 6.	5 2.3	14.0	16.3 2.5	2.5	127
705	E3	2		531.0	42.5		375.8		90.7				9.3 7.			16.4 2.3	2.9	125
706	E3	2	DH91	738.6	42.0		523.4		101.5				11.2 6.			15.8 2.5	3.0	128
707	E3	2	DH92		41.2		599.8		94.3				10.6 7.			15.2 2.2	2.9	127
708	E3	2	DH93	966.8	58.1			31.2	91.5			19.1				16.8 2.2	3.6	124
709 710	E3 E3	2 2	DH94 DH95	913.9 984.6	40.7 36.4		696.6 791.5		103.6 96.7			18.2 19.1				16.3 2.3 15.6 2.1	2.7 2.6	129 122
711	E3	2	DH95 DH96		39.2		629.0		104.4				11.3 6.			13.0 2.1	2.0 3.1	122
712	E3	2	DH97	714.0	39.5		534.1		105.4				8.7 6.			16.4 2.4	2.6	126
713	E3	2	DH98	878.0	48.7		487.5		88.6				10.0 8.			15.3 1.9	3.2	119
714	E3	2	DH99		49.9		435.1			17.9		27.4				17.1 2.4	3.1	131
715	E3	2	DH100	681.8	56.0	1.6	430.9	29.1	86.2	15.4	1.6	19.4	9.8 7.	1 1.3	16.0	17.3 2.5	3.5	126
716	E3	2	DH101	685.4	53.2	1.6	434.6	30.7	96.9	17.5	1.7	23.6	10.2 7.	7 0.5		16.5 2.1	3.3	124
717	E3	2	DH102		50.6		538.7		104.5				10.5 8.			19.7 2.4	2.8	130
718	E3	2	DH103		37.5		453.8		88.0				9.5 6.			16.1 2.4	2.7	132
719	E3	2	DH104		45.8		436.2		100.8				13.1 7.			17.1 2.4	2.9	131
720 721	E3 E3	2 2	DH105 DH106		42.5 52.2		721.2 422.3	30.4 31.0	102.7 96.1				10.7 6. 9.4 7.			16.5 2.7 17.6 2.3	3.0 3.3	127 128
721	E3	2	DH100 DH107		37.8		702.0		103.3				10.2 6.			17.0 2.3	2.8	128
723	E3	2	DH107		38.4		536.4		105.6				9.5 6.4			15.9 2.5	2.8	123
724	E3	2	DH109		40.3		588.6		95.5				10.7 7.			16.6 2.3	2.7	128
725	E3	2	DH110		45.9		497.6		101.7	16.4	1.6	21.1	10.1 7.			16.2 2.0	3.1	127
726	E3	2	DH111	696.0	50.1	1.6	436.9	30.1	104.5	19.2	1.7	25.6	11.5 8.	1 1.2	15.9	17.1 2.1	3.1	127
727	E3	2	DH112		43.2	1.4	353.8	31.9	98.1	16.0	1.6	20.7				17.1 2.3	2.9	127
728	E3	2	DH113		46.8		499.0		113.5				11.2 7.			16.4 2.3	3.2	127
729	E3	2	DH114		40.6		634.3			16.5			10.2 7.			16.0 2.2	2.8	126
730	E3	2		544.1			508.0						10.6 7.			15.7 2.2	2.7	127
731 732	E3 E3	2 2	DH116 DH117				702.5 775.8		101.6				9.9 6. 9.0 7.			14.9 2.3 15.2 2.2	2.7 2.4	126
733	E3	2	DH119		34.0 46.6		429.5		91.8 106.3			28.5	10.6 7.	1 1.2		13.2 2.2 18.1 2.3	2.4 2.9	124 128
734	E3	2	DH120		38.5		691.7		94.7				11.1 6.			16.6 2.5	2.7	129
735	E3	2	DH120 DH121		42.2		444.6						8.7 7.			17.4 2.5	2.9	131
736	E3	2	DH122		46.0		477.5		97.1	19.4			13.5 7.			17.1 2.4	2.9	131
737	E3	2	DH123		40.3		510.4		99.8	19.2			12.8 7.			16.0 2.1	2.8	127
738	E3	2	DH124	637.1	40.1		466.8	31.4		19.5			11.7 7.		14.9	$16.8\ 2.2$	2.7	131
739	E3	2	DH125		43.2		602.3		93.7				9.6 6.			14.9 2.2	3.1	127
740	E3	2	DH126		43.7		583.8		85.8				11.2 7.			17.5 2.3	2.7	130
741	E3	2	DH128		36.6		445.1		98.4				13.0 6.			16.6 2.5	2.6	131
742 743	E3	2	DH129		46.5		568.3		104.2				10.8 7.			16.5 2.3	3.2	126
743 744	E3 E3	2 2	DH130 DH131		44.6 41.3		660.1 283.0		94.3 99.1	17.5			10.9 8. 9.2 7.			17.6 2.2 18.8 2.4	2.7 2.6	126 132
/ ++	ц,	4	11131	404.4	тı.J	1.7	205.0	כ.דכ	<i>))</i> .1	10.9	4.1	51.0	1.4 1.	5 5.0	13.0	10.0 2.4	2.0	132

Table E.1 Continued.

No.	Env.	Rep.	Name	GYLD	GPS	GWPS	SPSM	TGW	PHT	FLL	FLW	FLA	FLS	SL	SSN	FSN	TSN	SC	GSP	HD
745	E4	1	DH1	671.4		1.0	671.4	28.8		12.5		12.4		6.0		12.7		2.2		139
746	E4	1	DH3	523.2		1.0	519.0					19.6				12.7				142
747	E4	1	DH4		27.9	0.8	753.2	30.0		13.9	1.6	17.6		6.4		13.1		2.5		142
748 749	E4 E4	1 1	DH5 DH6	633.9 665.9	38.6	1.0 1.0	608.9 667.9	29.0 31.1	75.1	13.1	1.5 1.2	17.9 13.1		7.5 6.6	1.4 1.6	13.7 13.5		2.0 2.3		142 136
749	E4 E4	1	DH0 DH7	554.1		0.9	592.6		67.4			18.3		6.1		12.7				130
751	E4	1	DH8	671.1		1.0	669.1		84.0		1.5	18.7		6.6	1.6	12.9		2.2		139
752	E4	1	DH9	572.6		1.1	529.2		75.7		1.5	17.8		6.6		14.1		2.4		142
753	E4	1	DH11	744.5		1.5	485.0		95.9		1.3	15.4		8.7	1.3	15.9		2.0		139
754	E4	1	DH12	538.7	37.9	1.0	527.1	28.4	62.0	11.5	1.7	15.6	6.7	5.7	0.6	14.1	14.7	2.6	2.7	141
755	E4	1	DH13	635.0	44.3	1.2	530.5	27.0	81.4	15.9	1.4	17.5	11.4	6.9		14.8		2.3	3.0	140
756	E4	1	DH14			1.4	491.8		81.3			18.4		7.3		15.4				139
757	E4	1	DH15			1.1	653.5		76.3			13.1				14.6			2.7	137
758	E4	1	DH16			0.9	544.3		70.1		1.3	17.1		6.2		13.2				139
759	E4	1	DH17	705.5		1.2	594.8		80.6		1.3	15.3		6.9		13.4				136
760 761	E4 E4	1 1	DH18	621.3 617.6		1.3 1.0	475.8 597.3		78.5 72.1		1.9 1.5	25.6 17.0		7.7 6.3		16.2 12.9				142 138
762	E4	1		483.6		1.0	448.2		73.9		1.6	22.2		6.4		14.1				143
763	E4	1	DH21	746.5		1.1	668.9		85.2		1.4	18.0		7.0		13.9				141
764	E4	1	DH22			1.2	581.5		87.7		1.5	17.5		6.8	0.9	14.5		2.3		141
765	E4	1	DH23	648.3		1.0	667.7	25.9	78.8	14.9	1.1	13.0		6.1		13.3				138
766	E4	1	DH24	615.4	34.6	0.9	672.6	27.1	74.4	16.1	1.6	20.9	9.8	6.1	1.2	12.8	14.0	2.3	2.7	138
767	E4	1	DH25	639.5	39.9	1.1	599.3	30.1	71.9		1.4	17.9	10.9	6.9		14.1		2.3	2.8	139
768	E4	1	DH26	707.5		1.1	643.8	27.9		13.6	1.4	14.6		6.6		14.3		2.2		139
769	E4	1	DH27			1.0	591.7		74.5			19.2		6.0		12.8				142
770	E4	1	DH28	621.1		1.1	558.5		80.5			17.0		6.2		13.5				141
771 772	E4 E4	1	DH29 DH30			1.0	673.5 544.5		69.1			14.3		6.6 6.8		13.1		2.2		141 142
773	E4 E4	1	DH30 DH31			1.0 1.1	544.5 524.9		73.8 75.8			19.9 15.5		0.8 7.0		13.9 14.4				142 140
774	E4	1		570.6		0.9	657.3		75.5			17.7		6.1		13.1				140
775	E4	1	DH32	506.9		0.9	591.5		84.1		1.7	21.0		7.0	2.1	15.9				144
776	E4	1	DH34			1.4	544.7		83.4		1.5	22.3		7.8		16.0				140
777	E4	1	DH35	595.9	30.2	0.9	678.6	29.3		13.9	1.5	16.1		6.0		11.7		2.2	2.6	139
778	E4	1	DH36	741.5	37.5	1.1	679.7	28.6	79.2	16.0	1.6	20.2	10.1	7.3	1.3	14.4	15.7	2.1	2.6	141
779	E4	1	DH37	590.1		1.0	597.8	25.8		17.7	1.4	19.8		6.6		13.5		2.3		142
780	E4	1	DH38	553.7		1.2	471.2		76.0		1.4	15.1		7.1	0.6	16.0				138
781	E4	1	DH39			1.1	605.3		72.7		1.4	18.1		5.6	0.8	13.3		2.5		139
782 783	E4	1 1	DH40			1.0	546.5		87.5			13.5		6.8	1.1	13.6				140
785 784	E4 E4	1	DH41 DH42	660.5 637.9		1.0 1.3	683.0 492.9		85.3 80.3		1.4 1.3	15.5 16.4		6.6 6.9		14.2 15.3		2.3		140 139
785	E4	1	DH42 DH43	769.0		1.5	647.3		71.8		1.3	15.2		6.5		13.2		2.3		139
786	E4	1	DH44	724.6		1.1	685.5		89.4			21.5		7.0		12.8				142
787	E4	1	DH45			0.9	653.3		78.8			14.4		6.6		13.0		2.3		139
788	E4	1	DH46	579.0	40.7	1.1	538.1	29.0	85.9	14.9	1.5	17.4	10.1	7.9	1.4	15.1	16.5	2.1	2.7	141
789	E4	1	DH47	726.0		1.1	639.1		82.8			14.3		6.8		13.4			3.1	141
790	E4	1	DH49			1.0	624.8		83.2			19.0		7.0		14.1				142
791	E4	1	DH50		35.6	1.0	589.7		81.8			13.7		6.5		13.8		2.3		141
792	E4	1		602.5		1.0	601.3									13.5				141
793	E4	1		725.7		0.9	774.5									14.8				138
794 795	E4 E4	1 1		647.2 663.5		1.0 1.5	618.8 448.6		70.4			15.1 19.5		6.8 7.8		14.5 14.8				139 139
796	E4	1		695.3		1.5	624.7		81.4			14.2				13.6				139
797	E4	1		638.6		1.1	544.9					14.2				13.6				138
798	E4	1		577.7		1.0	565.2					14.1				13.8				140
799	E4	1		723.0			679.5					13.0				12.6				138
800	E4	1	DH59	720.6	36.5	1.0	743.7	28.0	73.4	14.6	1.3	15.5	11.0	5.8		13.4			2.7	139
801	E4	1		681.5			595.2					15.8				12.8				139
802	E4	1		640.7		0.9	701.0					15.1		6.8		13.2				141
803	E4	1		666.2		1.2	577.3	29.0	74.2	14.9	1.4					12.9				138
804	E4	1		638.5		1.5	436.1					20.2		8.2		15.5				139
805 806	E4 E4	1		739.1			655.8 475.9									13.8				139 139
806	124	1	01103	529.2	44.0	1.1	475.9	27.0	74.9	17.3	1.4	10.9	12.0	1.4	1.1	15.4	10.3	4.2	2.9	139

Table E.1 Continued.

No.	Env.	Rep.	Name	GYLD	GPS	GWPS	SPSM	TGW	PHT	FLL	FLW	FLA	FLS SI	SSN	FSN	TSN SC	GSP	HD
807	E4	1	DH66	439.7	34.0		399.3			17.4			10.4 7.0			16.0 2.3	2.4	142
808	E4	1	DH67	588.6	35.7		586.3			14.3			10.4 6.1			14.4 2.3	2.6	138
809	E4 E4	1	DH68	438.6	38.0		455.9			16.0			10.0 6.			14.9 2.2	2.6	139
810 811	E4 E4	1 1	DH69 DH70	642.1 512.3	42.4 35.3		652.6 527.1			15.0 16.0			10.0 6.0 11.6 6.1			14.4 2.4 15.6 2.3	3.1 2.6	140 142
812	E4	1	DH70 DH71	683.9	39.6		605.2			14.0			9.5 7.5			15.8 2.1	2.6	141
813	E4	1	DH72	575.8	37.7		632.8			14.4			9.6 6.8			15.9 2.4	2.6	142
814	E4	1	DH73	479.5	34.2	0.9	524.1	26.6		16.4		18.7	11.5 6.4	1.6		15.3 2.4	2.5	142
815	E4	1	DH75	634.8	44.7		474.5			14.6			11.4 7.1			16.7 2.2	2.9	137
816	E4	1	DH76	659.1	34.1		690.2			14.3			10.2 6.2			14.2 2.3	2.6	139
817 818	E4 E4	1 1	DH77 DH78	573.3 659.7	34.4 40.0		545.5 566.8			20.1 17.9			14.9 7.3 13.3 7.1			15.5 2.1 16.0 2.3	2.5 2.8	140 137
819	E4 E4	1	DH78 DH79	761.2	40.0		523.5			16.0			12.0 7.3			15.5 2.1	2.8 3.4	137
820	E4	1	DH80	733.9	52.6		511.8			15.6			11.2 7.0			15.7 2.2	3.4	139
821	E4	1	DH81	520.4	35.8		508.7	30.3	66.0	15.2	1.7	20.4	9.1 6.0			15.2 2.3	2.5	140
822	E4	1	DH82	659.4	34.0		740.8			12.9		14.2				14.2 2.2	2.7	139
823	E4	1	DH83	619.2	35.1		532.9			14.6			11.0 6.			14.3 2.3	2.8	141
824	E4	1	DH84	747.9	36.0		661.3			11.6		11.3				14.6 2.2	2.7	136
825 826	E4 E4	1 1	DH85 DH86	665.8 635.8	35.7		683.6 572.2			13.8 13.2			9.9 6.0 10.4 6.1			14.7 2.2 14.6 2.4	2.6 2.9	139 139
820	E4 E4	1	DH87	742.9	39.8 44.4		651.1			15.2			11.3 6.0			15.3 2.3	2.9 3.0	139
828	E4	1	DH89	587.0	37.6		526.0			13.4			10.1 6.5			16.1 2.5	2.6	139
829	E4	1		545.1	35.3		534.4			14.8			11.1 6.			16.1 2.4	2.5	137
830	E4	1	DH91	559.8	40.4	1.1	497.6		82.1	15.2	1.3	15.6	11.9 6.3	3 1.4	13.9	15.3 2.4	2.9	139
831	E4	1	DH92	663.3	36.4		711.7			13.4			10.1 6.3			14.2 2.3	2.8	140
832	E4	1	DH93	635.5	50.9		486.6			16.5			11.5 7.5			16.7 2.2	3.2	139
833	E4 E4	1	DH94	748.6 674.1	35.1		736.1			12.3			9.1 6.0			15.3 2.3	2.5	138
834 835	E4 E4	1 1	DH95 DH96	605.7	35.4 32.7		630.0 568.2			15.6 14.8			10.4 7.2 11.4 6.3			15.6 2.2 12.8 2.0	2.5 2.8	138 138
836	E4	1	DH90 DH97	672.5	36.9		580.8			14.7			9.2 6.3			14.5 2.3	2.8	138
837	E4	1	DH98	726.1	42.4		578.1			14.2			10.4 7.3			15.3 2.1	2.9	136
838	E4	1	DH99	671.3	39.2		601.0	29.5	77.2	16.2	1.5		10.9 6.0			14.4 2.2	2.8	141
839	E4	1	DH100		48.0		594.6			15.3			10.2 6.8			15.7 2.3	3.2	139
840	E4	1	DH101		44.8		634.7			13.7			9.7 7.2			15.3 2.1	3.0	138
841	E4 E4	1	DH102		44.5		576.9			16.8			11.5 7.4			15.7 2.1	3.0	142
842 843	E4 E4	1 1	DH103 DH104		33.4 39.6		623.9 575.1			15.8 18.1			9.3 6.9 13.1 6.1			15.9 2.3 14.5 2.4	2.4 3.0	142 142
844	E4	1	DH104		39.6		665.7			16.0			11.7 5.8			14.7 2.6	3.0	140
845	E4	1	DH106		42.8		582.9	28.7		14.8			9.7 7.			16.1 2.3	2.9	139
846	E4	1	DH107		36.0	1.0	609.6	28.2	75.7	13.0	1.3	13.1	10.2 6.5	5 0.8	12.8	13.6 2.1	2.8	139
847	E4	1	DH108		36.3		602.8			15.6			12.3 5.9			13.7 2.3	2.9	139
848	E4	1	DH109		38.0			26.8		15.5			10.7 7.0			15.3 2.2	2.7	139
849 850	E4 E4	1 1	DH110 DH111		41.1 43.8		570.4 529.4			13.7 16.1			11.3 7.0 11.7 7.2			15.2 2.0 15.2 2.1	2.9 3.1	137 139
850	E4 E4	1	DH112		45.0		460.9			15.3			11.7 7.0			15.2 2.1	3.1	139
852	E4	1	DH112 DH113		33.2		752.3			13.5			9.6 5.9			14.5 2.5	2.5	139
853	E4	1	DH114		34.6	0.9	576.8			13.8		16.6			13.2	13.9 2.1	2.6	140
854	E4	1		576.7			537.4						10.5 6.2			15.0 2.2	2.6	139
855	E4	1	DH116		31.2		554.3		72.7				10.4 6.			13.8 2.3	2.6	140
856	E4	1	DH117		33.0		505.8		64.8				9.6 6.5			13.7 2.1	2.6	138
857	E4	1	DH119		39.9		445.6			16.7 14.9			10.8 7.2			16.9 2.3	2.6	142
858 859	E4 E4	1 1	DH120 DH121		35.1 36.2		589.2 697.7		77.9				11.0 6.0 10.5 6.8			13.9 2.3 15.4 2.3	2.7 2.7	141 141
860	E4	1	DH121 DH122		39.3		674.4			15.2			11.0 6.4			15.4 2.5	2.7	141
861	E4	1			44.2		544.8		81.9				13.5 7.2			15.3 2.1	3.1	142
862	E4	1	DH124		37.1		646.6		72.4				11.8 7.0			15.4 2.0	2.6	141
863	E4	1	DH125		39.7		576.7			13.6			9.1 6.1			14.6 2.2	2.9	140
864	E4	1		637.4			601.8			15.2			9.8 7.4			16.5 2.2	2.7	142
865 866	E4 E4	1	DH128 DH129	594.2	40.7 40.9		585.4 510.5		81.8	17.7 13.9			13.4 6.2 10.3 6.0			15.3 2.5 14.8 2.3	2.9	140
860 867	E4 E4	1 1	DH129 DH130		40.9 37.5		670.7			13.9			9.1 6.8			14.8 2.3	3.1 2.9	140 139
868	E4	1	DH130		36.0		515.3			17.1			10.3 7.3			16.8 2.3	2.5	142

Table E.1 Continued.

No.	Env.	Rep.	Name	GYLD	GPS	GWPS	SPSM	TGW	PHT	FLL	FLW	FLA	FLS	SL	SSN	FSN	TSN	SC	GSP	HD
869	E4	2	DH1	591.6		1.2	486.9	29.0		13.4		13.8		6.4	0.2	13.9		2.2	3.2	139
870	E4	2	DH3	584.3		1.2	491.4		77.0			18.9		6.2	0.6		14.2			141
871 872	E4 E4	2 2	DH4 DH5	495.7 541.2		0.9 1.2	555.8 442.0	29.0	70.9 71.5		1.5 1.5	15.3 16.9		6.1 7.5	1.5	13.1 14.2		2.4 2.0		141 141
872	E4 E4	2	DH5 DH6	614.4		1.2	504.5	30.5	75.8		1.5	17.4		6.6		14.2		2.0		137
874	E4	$\frac{1}{2}$	DH7	575.8		0.9	616.5		72.6		1.6	20.4		6.5		14.3		2.6		143
875	E4	2	DH8	697.5	45.5	1.2	561.1		77.4		1.4	18.8		7.1	0.6	13.8		2.0	3.3	140
876	E4	2	DH9	557.6		1.4	403.2		75.0		1.5	16.2		7.2	1.5	15.8		2.4		142
877	E4	2	DH11	577.7	38.2	1.3	451.7	32.9	85.5		1.4	19.1		7.7	2.0	14.2		2.1		137
878 879	E4 E4	2 2	DH12 DH13	379.3		1.1 1.2	355.8 459.6	27.4 25.8	52.7 77.1		1.6	15.6 22.0		6.1 7.0	0.6 1.3	13.7 15.1		2.4 2.4		142 142
880	E4 E4	2	DH13 DH14	539.5 703.3		1.2	459.0		78.0		1.6 1.5	17.9		7.0		15.1				142
881	E4	$\frac{2}{2}$	DH15	592.8		1.1	545.3		75.6			12.7		6.8		14.5				137
882	E4	2		580.0		1.5	398.1		74.2			17.7		7.4		16.0				137
883	E4	2	DH17	665.4	44.5	1.5	453.0		76.1		1.2	13.1	10.9	7.2	0.9	14.4		2.1	3.1	137
884	E4	2	DH18	553.9		1.4	406.0	28.7			1.9	26.8		7.7		16.1				142
885	E4	2	DH19			1.1	500.8		73.2		1.5	14.5		6.4	1.1	12.7		2.2		137
886 887	E4 E4	2 2	DH20 DH21			1.3 1.2	464.1 500.5		74.7 78.7		1.6 1.5	19.6 19.5		7.1 7.1	1.0 2.1	15.5		2.3 2.3		142 142
888	E4 E4	2	DH21 DH22			1.4	457.5	30.3		15.0	1.5	19.5		7.3	1.3	15.9		2.3		142
889	E4	$\frac{1}{2}$	DH23			1.3	497.5		79.9		1.3	16.9		6.8		14.9				140
890	E4	2	DH24			1.2	558.2		79.5		1.5	16.1	8.6	6.7		14.2		2.2	3.1	139
891	E4	2	DH25	588.4	36.8	1.0	561.4	32.0	69.7		1.4	15.4	10.3	6.4	1.8	12.8		2.3	2.8	139
892	E4	2	DH26	578.6		1.1	518.0	27.7	77.0		1.5	20.0		7.0	1.4	14.7		2.3		140
893	E4	2	DH27			1.1	503.1		75.1		1.4	16.9		6.1	1.3	13.2		2.4		142
894 895	E4 E4	2 2	DH28 DH29	680.7 626.3		1.3 1.0	523.2 599.9		81.4 69.0		1.3	15.0 16.3		6.5 7.0		13.6 13.2				140 140
895	E4 E4	2	DH29 DH30			1.0	556.6	31.2			1.4	19.9		6.9	0.9	15.2		2.1		140
897	E4	2	DH31	495.4		1.1	434.2		74.9			18.2		7.3		14.4				142
898	E4	2		520.6		0.9	564.0		78.2			13.5		6.4		14.4				143
899	E4	2	DH33	573.3	45.5	1.1	509.6	26.8	85.2	16.3	1.6	20.9	10.1	6.8	1.5	15.8	17.3	2.5	2.9	145
900	E4	2	DH34			1.3	522.3		83.8		1.3	13.5		7.3		15.9		2.3		139
901	E4	2	DH35	552.5		1.1	482.1		72.6		1.5	16.2		6.9		13.6		2.1		138
902 903	E4 E4	2 2	DH36 DH37	652.8 550.2	39.9	1.2 1.2	558.4 478.0	30.3 29.4	75.1	15.7	1.6 1.2	20.0 15.0		7.5 6.8	1.0 1.1	14.8 14.4		2.1 2.3		141 140
904	E4	2	DH38	622.8		1.2	488.4		73.2			17.4		7.5	0.7		17.0			138
905	E4	2	DH39		38.3	1.2	511.4	29.7	71.1		1.2	12.3		5.5	0.9	12.7		2.5		139
906	E4	2	DH40	524.8	35.3	1.0	504.1	29.7	81.8	16.4	1.5	19.2	11.0	7.1	0.8	14.0	14.8	2.1	2.5	142
907	E4	2	DH41	720.2		1.1	631.8	28.9		16.0	1.5	19.6		7.2	1.1	14.6		2.2		142
908	E4	2	DH42			1.1	537.7	28.7		16.2	1.4	17.7			1.1		15.0			140
909 910	E4	2 2	DH43	649.7 751.4		0.9	686.8 641.7	29.9		14.6	1.3	15.1 19.5		5.8 7.2		11.8 13.3		2.3		139 142
910	E4 E4	2	DH44 DH45		30.0	1.2 1.0	578.0		86.8 75.3			19.5		6.3		12.1		2.0		142
912	E4	2	DH46	528.6		1.1	501.5	29.5		17.0	1.5	19.8		7.3		13.8				141
913	E4	2	DH47	690.0	43.2	1.2	558.3		79.4		1.4	13.8		6.9	0.9	14.7		2.3	2.9	141
914	E4	2	DH49	585.8	40.3	1.1	524.5	31.1	80.4	15.2	1.3	16.2	11.4	6.7	1.4	13.8	15.2	2.3	2.9	141
915	E4	2	DH50		31.9	1.0	603.5		81.9			13.8		6.1	1.3	12.7		2.3		140
916	E4	2		564.7		1.0	575.7									14.9				142
917 918	E4 E4	2 2		720.3 534.4		0.9	759.0 469.6					13.7				13.7 14.8				139 141
918	E4 E4	2		570.0		1.1 1.1	501.8					14.5				13.3				139
920	E4	2		596.8		1.2	495.7					13.6		6.5		14.7				139
921	E4	2		632.9		1.3	494.9					16.3		6.6		13.4				140
922	E4	2	DH57	551.5	38.6	1.1	486.8	28.5	74.1	12.8	1.4	14.2	9.2	6.0	0.7	13.9	14.6	2.4		139
923	E4	2		632.5		1.1	570.4									13.3				139
924	E4	2		757.5		1.1	678.7					14.6				14.0				139
925 926	E4 E4	2 2		607.4 605.5		1.3 1.1	458.0 560.1									13.5 14.6				140 142
920 927	E4 E4	2		514.4		1.1	440.4									14.0				142
928	E4	2		539.9		1.5	351.9									16.2				139
929	E4	2		764.0			563.8									14.5				138
930	E4	2	DH65	587.2	55.8	1.5	389.7	27.2	74.8	16.8	1.3	17.9	12.6	8.3		17.0			3.3	138

Table E.1 Continued.

No.	Env.	Rep.	Name	GYLD	GPS	GWPS	SPSM	TGW	PHT	FLL	FLW	FLA	FLS SL	SSN	FSN	TSN SC	GSP	HD
931	E4	2	DH66	600.6	41.2		494.7			16.5			10.1 7.6			17.3 2.3	2.7	143
932	E4	2	DH67	586.4	35.7		544.0			13.0			10.7 6.3			14.5 2.3	2.6	138
933 934	E4 E4	2 2	DH68 DH69	389.7 585.2	36.4 43.2		435.9 484.4			16.5 14.2			10.8 6.6 10.5 6.6			14.8 2.2 15.2 2.3	2.6 3.0	139 140
934	E4 E4	2	DH70	585.2	4 <i>3</i> .2 34.7		548.8			14.2			11.2 6.8			16.2 2.4	3.0 2.4	140
936	E4	2	DH71	531.8	36.0		479.1			14.9			10.5 6.6			13.8 2.1	2.7	142
937	E4	2	DH72	578.4	41.6		515.1			15.5		19.1	10.0 7.2		15.6	16.8 2.3	2.7	142
938	E4	2	DH73	637.7	43.9		508.2			13.7			9.2 7.2			16.5 2.3	2.8	141
939	E4	2	DH75	725.4	41.6		551.2			15.3			10.9 7.5			16.1 2.2	2.8	137
940 941	E4 E4	2 2	DH76 DH77	531.9 599.9	38.2 40.6		493.0			14.0 14.2			10.0 6.4			13.9 2.2	2.9 2.6	140 140
941 942	E4 E4	2	DH78	736.2	40.0		478.8 572.1			14.2			12.2 7.9 12.6 7.3			17.1 2.2 16.2 2.2	2.0 3.0	140
943	E4	2	DH79	643.6	39.1		563.6			14.2			10.8 6.5			14.8 2.3	3.0	137
944	E4	2	DH80	660.4	45.3		484.5			15.2			11.4 6.7			14.9 2.2	3.2	139
945	E4	2	DH81	525.3	39.9	1.2	444.4	30.4	72.2	14.6	1.6	18.4	9.5 6.8	0.5	14.9	15.4 2.3	2.7	140
946	E4	2	DH82	567.5	40.6		490.1			13.7			10.0 6.9			15.1 2.2	2.8	138
947	E4	2	DH83	615.3	27.2		681.4			13.8			11.3 5.5			13.2 2.4	2.6	141
948	E4	2	DH84	617.8	38.8		488.8			12.9			11.1 7.2			14.3 2.0	2.9	136
949 950	E4 E4	2 2	DH85 DH86	662.2 647.5	40.1 41.5		560.7 582.8			17.7 13.9			11.8 6.5 10.9 6.1			14.3 2.2 14.7 2.4	2.9 3.0	$\begin{array}{c} 140 \\ 140 \end{array}$
950 951	E4	2	DH87	581.6	40.3		512.8			13.4			10.3 6.2			13.8 2.2	3.1	139
952	E4	2	DH89	588.1	33.1			31.8		13.1			9.7 6.0			14.0 2.3	2.6	141
953	E4	2	DH90	488.7	43.9	1.3	364.5		71.0	13.6	1.2		11.7 7.5			17.1 2.3	2.7	137
954	E4	2	DH91	671.3	39.2	1.1		29.8	84.0	14.3	1.3	15.2	10.7 6.4	1.2	14.1	15.3 2.4	2.8	139
955	E4	2	DH92	518.8	31.4		560.9			13.4			10.5 6.0			13.7 2.3	2.6	140
956	E4	2	DH93	559.0	49.5		423.2			14.3			11.0 7.4			16.3 2.2	3.2	139
957 958	E4 E4	2 2	DH94 DH95	662.9 587.8	38.9 32.8		579.4 579.7			13.3 12.3			10.6 6.9 9.6 6.5			16.2 2.3 13.9 2.2	2.6 2.6	139 139
958 959	E4 E4	2	DH95 DH96	719.5	35.4		601.1			12.5			10.6 6.5			13.9 2.2	2.0	139
960	E4	2	DH97	604.5	45.7		436.2			14.8			9.2 7.1			15.7 2.2	2.9	139
961	E4	2	DH98	566.3	32.4		518.6			13.8			10.9 6.4			13.5 2.1	2.7	137
962	E4	2	DH99	672.8	40.4	1.2	570.1		71.9	13.7	1.5		9.4 6.6	0.4	13.7	14.1 2.2	2.9	141
963	E4	2	DH100		45.9		378.3			11.4		11.2		1.0		16.2 2.3	3.0	138
964	E4	2	DH101		39.9		508.8			12.4			9.2 6.6			13.8 2.1	3.0	138
965 966	E4 E4	2 2	DH102 DH103		42.8 37.0		454.1 518.1	26.8		14.8 16.5			10.7 7.1 10.1 7.0			15.0 2.1 15.6 2.2	3.1 2.6	142 142
960 967	E4	2	DH103		45.5		583.1			16.2			11.4 6.9			16.3 2.4	3.0	142
968	E4	2	DH105		45.6		553.6			16.6			11.1 6.2			15.7 2.5	3.1	140
969	E4	2	DH106	561.9	47.3	1.3	428.9	27.8	74.3	13.7	1.6	17.4	8.6 6.9	0.8	14.6	15.4 2.2	3.2	140
970	E4	2	DH107		38.3		594.4			14.5			10.3 7.0			14.6 2.1	2.8	139
971	E4	2	DH108		42.6		572.9			14.3			11.7 7.0			16.4 2.3	2.8	137
972	E4	2	DH109		41.9		453.9			15.9			10.5 7.7			16.1 2.1	2.8	141
973 974	E4 E4	2 2	DH110 DH111		43.3 38.9		481.7 526.1			14.9 15.4			12.9 7.4 11.5 6.9			15.4 2.1 14.8 2.1	3.0 2.9	137 139
975	E4	2	DH112		38.7		497.2			12.1			9.0 6.6			15.1 2.3	2.9	139
976	E4	2	DH113		33.2		555.7			11.9			10.0 5.7			13.9 2.4	2.7	139
977	E4	2	DH114		40.5	1.2	447.7		63.2	13.1	1.5	15.1				14.9 2.1	2.8	140
978	E4	2	DH115		36.4		484.2					14.8	11.4 6.8	1.4		15.2 2.2	2.6	138
979	E4	2	DH116		33.1		650.7			12.6			9.7 6.3			14.4 2.3	2.6	139
980	E4	2	DH117		38.8		393.0		59.9				11.4 7.1			13.9 2.0	2.9	139
981 982	E4 E4	2 2	DH119 DH120		49.1 36.2		390.3 614.0			18.7 14.4			10.7 7.7 11.0 6.2			16.6 2.2 13.9 2.2	3.1 2.8	141 139
982 983	E4 E4	2	DH120 DH121		38.2		548.4		71.8				10.3 6.9			15.9 2.2	2.8	139
984	E4	2	DH122		40.9		547.4			14.6			10.5 6.6			16.1 2.4	2.7	142
985	E4	2	DH123		41.6		506.5			14.9			11.7 7.1			15.6 2.2	2.9	140
986	E4	2	DH124		42.8	1.2	549.9		77.5	16.0	1.4	18.0	11.3 7.7	1.3	14.6	15.9 2.1	2.9	143
987	E4	2	DH125		35.5		656.1		69.7				9.0 5.9			13.9 2.4	2.8	139
988	E4	2	DH126		44.9		533.2		71.8				9.6 7.8			16.8 2.2	2.8	142
989 990	E4 E4	2 2	DH128 DH129		46.0 44.0		480.0 535.1		71.6 83.8				11.3 6.4 10.8 6.9			15.4 2.4 15.5 2.2	3.3 3.1	142 138
990 991	E4 E4	2	DH129 DH130		44.0		480.2	27.2	85.8 73.1				9.7 7.3			15.3 2.2 15.4 2.1	5.1 2.9	138
992	E4	2	DH130		41.5		383.9			16.3			10.8 7.6			16.8 2.2	2.7	142

Table E.1 Continued.

994 E5 1 DH1 394 36.8 940.9 25.5 .	No.	Env.	Rep.	Name	GYLD	GPS	GWPS	S SPSM	TGW	PHT	FLL	FLV	V FLA	A FLS	SL	SSN	FSN	TSN SC	GSP	HD
995 E5 1 DH5 614 337 0.8 7.9 24.5 7.4 3.5 1.6 1.9 7.4 3.5 1.6 1.9 2.5 1.2 1.6 1.8 2.5 2.6 1.6 1.9 2.5 1.2 1.6 1.8 2.5 2.5 1.9 1.9 1.6 1.8 2.7 2.5 1.2 3.9 1.5 1.6 1.8 2.9 2.5 1.2 3.9 1.5 1.6 1.8 2.9 2.9 1.9 1.9 1.9 2.5 1.2 3.9 2.2 1.2 3.9 2.1 2.7 3.9 1.9 1.2 2.1 2.7 1.9 1.9 1.8 2.2 1.5 1.0 1.5 1.0 1.5 1.2 2.7 1.7 1.6 1.8 2.2 2.2 1.6 1.8 1.2 2.2 1.1 1.6 1.2 2.2 1.6 1.1 1.6 1.1 1.5 1.1 1.1 1.1 1.1 1.1 1.1 1.1 1.1 1.1 1.1 1.										•				•						
996 ES 1 DH6 502 24.2 1.4 16.2 18.4 2.5 2.6 110 997 ES 1 DH6 502 42.3 1.4 426.2 27.9 1.7 3.2 1.6 19.9 2.5 1.3 1.6 1.9 2.5 2.5 2.3 1.0 1.5 1.0 1.6 1.8 2.7 2.9 1.9 1.0 1.5 1.0 1.6 1.8 2.7 2.9 1.9 1.2 1.1 1.0 1.0 1.5 1.0 1.1 2.85 2.1 7.5 1.8 2.2 2.5 2.7 1.5 1.0 1.1 2.2 1.2 2.1 7.5 1.8 1.2 2.1 7.5 1.8 1.2 2.1 7.5 1.8 1.2 2.2 2.2 1.2 1.1 1.0 <t< td=""><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td>•</td><td></td><td></td><td></td><td></td><td></td><td></td></t<>														•						
979E51DH749041911420279732.216182.52.5123999E51DH84395071.3338.1272791916.818.72.4301151000E51DH9404.757.01.5274.924.88.32.319.822.12.72.91191001E51DH1158.99.81.4440.033.28.62.71.51.81.81.22.51.11002E51DH1358.29.071.345.42.458.22.319.21.22.62.61.61004E51DH1663.73.71.51.44.40.03.67.77.42.81.41.62.22.61.11006E51DH1653.71.154.22.72.78.02.81.11.92.77.33.01.91010E51DH1264.740.31.254.43.17.77.53.71.51.81.61.42.22.61.11010E51DH2064.740.31.254.43.27.57.77.53.71.51.81.82.52.61.11010E51DH2064.740.31.254.														•						
998 E5 1 DH7 459.0 1.1 426.1 253 6.9 3.3 166 18.7 2.4 30 15 1000 E5 1 DH19 404.7 57.0 1.5 274.9 248.8 8.3 2.3 18.8 2.2 2.7 1.5 1001 E5 1 DH11 582.9 50.7 1.3 455.4 2.4 5.8 2.2 1.8 2.6 1.6 1.6 1.6 1.8 1.8 2.5 2.7 1.8 1.8 1.8 2.5 2.6 1.6 1.6 1.6 1.8 1.6 1.8 2.6 2.1 1.8 2.6 2.6 1.1 1.1 1.1 2.4 2.7 7.5 1.8 1.6 1.1 2.2 2.6 1.1 1.1 2.4 2.7 7.5 1.8 1.6 1.1 1.1 2.4 2.7 7.5 3.1 1.1 1.2 2.4 2.1 2.6 1.1 1.0 1.1 1.1 1.1 1.1 1.1 1.1 1.1 <td></td>																				
999ES111338.127277919168.72.43.01151000ES1DH1588.9398.144400.3328.82.3198.22.12.72.91191001ES1DH11588.9398.144400.3328.62.7157.182.12.51.61002ES1DH13582.950.71.3455.42.17.71.81.82.22.62.61.61004ES1DH1664.2409.111.442.47.87.51.81.51.72.22.61.11006ES1DH17486.53.71.241.32.787.12.61.41.02.22.61.11007ES1DH17485.33.61.18.22.71.81.81.11.92.73.01.91008ES1DH1185.53.51.12.77.53.71.11.92.73.01.11010ES1DH21647.12.31.27.53.71.51.81.82.22.61.11011ES1DH2257.54.71.23.14.87.62.51.51.81.41.92.51.61.11.11.41.4																				
1001 E5 1 DH11 598.9 398 14 4400 332																				
1003 E5 1 DH13 582.9 507 1.3 4554 245 8.2 2.3 P.2 15 2.6 2.6 16 100 E5 1 DH15 604.2 409 1.1 542 278	1001	E5	1	DH11	598.9	39.8	1.4	440.0	33.2						8.6	2.7	15.7	18.4 2.1	2.5	114
1004 E5 1 DH14 639. 1 81 12 515. 31.7 , 74 2.9 18.8 2.5 2.4 16 100 E5 1 DH15 60.2 40 9.1 542. 47.8 , 71 2.6 14.3 16.9 2.4 2.6 111 1007 E5 1 DH15 63.5 97.1 2 421.5 30.8 , 71 2.6 14.3 16.9 2.4 2.6 121 100 E5 1 DH18 53.5 94.7 1.2 421.5 30.8 , 7.4 2.8 14.1 7.2 2.3 2.6 112 1008 E5 1 DH18 53.5 94.7 1.2 421.5 30.8 , 7.4 2.8 14.1 7.2 2.3 2.6 113 100 E5 1 DH12 64.5 36.5 1.1 58.7 2.9.7 , 8.8 2.8 17.5 20.3 2.5 2.7 123 100 E5 1 DH12 64.7 40.3 1.2 554.4 31.2 , 7.5 3.7 15.1 18.8 2.5 2.6 118 101 E5 1 DH12 57.5 4.6 7 1.2 43.1 25.0 , 7.3 2.4 17.1 19.5 2.5 2.6 118 101 E5 1 DH12 51.7 47.0 1.2 43.1 24.8 , 7.0 1.8 18.2 2.3 2.6 17.8 101 E5 1 DH12 52.5 40.1 1. 560.8 28.8 , 6.9 2.5 14.3 16.8 4.2 4.2 8 111 101 E5 1 DH12 52.5 40.1 1.0 535.5 25.0 , 7.5 2.5 15.7 18.2 2.4 2.5 111 101 E5 1 DH12 542.5 40.1 1.0 535.5 25.0 , 7.5 2.5 15.7 18.2 2.4 2.5 111 101 E5 1 DH12 542.5 40.1 1.0 480.0 22.2 , 7.6 2.1 16.3 18.4 2.4 2.9 115 101 E5 1 DH22 542.4 0.1 1.0 482.6 29.0 , 6.3 3.3 142 17.5 2.5 2.5 11 101 E5 1 DH12 540.1 40.1 428.1 30.7 , 6.9 3.0 14.1 71.7 2.6 2.7 117 102 E5 1 DH12 540.6 1.1 40.4 2.1 29.8 2.6 8 , 7.7 2.4 16.0 19.0 2.5 2.4 116 102 E5 1 DH12 50.6 46.0 1.1 428.1 30.7 , 7.9 2.4 17.0 19.2 3.2 7 16 101 E5 1 DH12 50.6 46.1 1 40.4 24.8 , 7.7 2.4 16.0 19.0 2.5 2.4 116 102 E5 1 DH13 469.5 40.0 1.1 428.1 30.7 , 7.9 2.4 17.0 19.2 3.2 7 16 102 E5 1 DH13 548.0 35.7 1.1 517.5 30.3 , 7.9 2.4 17.0 19.2 3.2 7 116 102 E5 1 DH13 548.0 35.7 1.1 517.5 30.3 , 7.9 2.4 17.0 19.2 3.2 7 116 102 E5 1 DH13 548.0 35.7 1.1 517.5 30.3 , 7.9 2.4 12.0 17.8 2.4 2.4 115 102 12 55 1 DH13 548.0 35.7 1.1 517.5 30.3 , 7.9 1.9 20.2 2.1 2.8 2.9 123 102 15 5 1 DH13 548.0 35.7 1.1 517.5 30.3 , 7.9 2.4 16.0 17.8 2.4 2.4 115 102 E5 1 DH13 648.2 45.9 1.3 515.1 29.6 , 7.7 1.8 16.2 18.0 2.3 2.8 110 102 E5 1 DH13 648.2 45.9 1.3 515.1 29.6 , 7.7 1.8 16.2 18.0 2.3 2.8 110 102 E5 1 DH13 648.2 45.9 1.3 515.1 29.6 , 7.7 1.8 16.2 18.0 2.3 2.8 110 102 E5 1 DH13 648.2 45.9 1.2 446.2 14.4 11.1 437.5 2.4 14.4 110 12.5 11013 14.5 12.5 10 1113 14.5 12.5 10 1113 14.5 12.5 10 1113 14.5 12.5	1002	E5	1	DH12	288.8	43.3	1.0								7.3	1.9	16.3	18.2 2.5	2.7	115
1005 E5 1 DH15 (042 409 1.1 542 47.8 75 1.8 17.2 2.3 2.6 111 1006 E5 1 DH16 37.1 37.5 1.0 5415 27.8 71 2.6 14.3 16.9 2.5 2.4 2.6 111 1007 E5 1 DH19 6345 3.65 1.1 2 443.0 27.5			1																	
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1000 E5 1 DH19 6345 365 1.1 582.7 29.7																				
1012 E5 1 DH22 597.5 46.7 1.2 516.4 26.3	1011	E5	1	DH21	664.7	40.3	1.2								7.5	3.7			2.6	118
	1012	E5	1	DH22	597.5	46.7	1.2	516.4	26.3						8.2	2.3	18.2	20.5 2.5	2.6	116
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1045 E5 1 DH56 643.6 37.4 1.2 554.8 29.4 . . . 6.9 2.2 14.2 16.4 2.4 2.6 114 1046 E5 1 DH57 402.5 36.1 0.9 467.5 22.8 . . . 6.7 2.4 15.8 18.2 2.7 2.4 115 1047 E5 1 DH58 584.9 37.9 1.1 554.9 28.4 . . . 6.8 2.3 13.7 16.0 2.4 2.8 114 1048 E5 1 DH59 581.6 39.1 1.0 592.9 24.4 . . . 6.5 1.7 14.1 15.8 2.4 2.7 109 1049 E5 1 DH60 568.4 48.2 1.4 406.6 27.9 . . 8.0 2.2 15.9 18.1 2.3 3.0 110 1050 E5 1 DH61 595.6 42.1 1.2	1043	E5		DH54	612.7	47.9	1.6								8.3	1.9			3.0	110
1046 E5 1 DH57 402.5 36.1 0.9 467.5 22.8 . . . 6.7 2.4 15.8 18.2 2.7 2.4 115 1047 E5 1 DH58 584.9 37.9 1.1 554.9 28.4 . . . 6.8 2.3 13.7 16.0 2.4 2.8 114 1048 E5 1 DH59 581.6 39.1 1.0 592.9 24.4 . . . 6.5 1.7 14.1 15.8 2.4 2.7 109 1049 E5 1 DH60 568.4 48.2 1.4 406.6 27.9 . . 8.0 2.2 15.9 18.1 2.3 3.0 110 1050 E5 1 DH61 595.6 42.1 1.2 503.1 27.0 . . 7.4 2.2 15.8 18.0 2.4 2.7 120 1051 E5 1 DH62 228.7 41.4 0.7 308.6 <td></td> <td></td> <td>1</td> <td></td> <td>7.2</td> <td></td> <td></td> <td></td> <td></td> <td>116</td>			1												7.2					116
1047E51DH58584.937.91.1554.928.46.82.313.716.02.42.81141048E51DH59581.639.11.0592.924.46.51.714.115.82.42.71091049E51DH60568.448.21.4406.627.98.02.215.918.12.33.01101050E51DH61595.642.11.2503.127.07.42.215.818.02.42.71201051E51DH62228.741.40.7308.618.37.01.615.316.92.42.71151052E51DH63547.154.91.5361.928.18.61.617.218.82.23.21101053E51DH64590.238.71.2504.833.17.92.015.817.82.32.4112																				
1048E51DH59581.639.11.0592.924.46.51.714.115.82.42.71091049E51DH60568.448.21.4406.627.98.02.215.918.12.33.01101050E51DH61595.642.11.2503.127.07.42.215.818.02.42.71201051E51DH62228.741.40.7308.618.37.01.615.316.92.42.71151052E51DH63547.154.91.5361.928.18.61.617.218.82.23.21101053E51DH64590.238.71.2504.833.17.92.015.817.82.32.4112												•								
1049E51DH60568.448.21.4406.627.98.02.215.918.12.33.01101050E51DH61595.642.11.2503.127.07.42.215.818.02.42.71201051E51DH62228.741.40.7308.618.37.01.615.316.92.42.71151052E51DH63547.154.91.5361.928.18.61.617.218.82.23.21101053E51DH64590.238.71.2504.833.17.92.015.817.82.32.4112										•		•	•							
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1052 E5 1 DH63 547.1 54.9 1.5 361.9 28.1 . . . 8.6 1.6 17.2 18.8 2.2 3.2 110 1053 E5 1 DH64 590.2 38.7 1.2 504.8 33.1 . . . 7.9 2.0 15.8 17.8 2.3 2.4 112											•	•	•							
1053 E5 1 DH64 590.2 38.7 1.2 504.8 33.1 7.9 2.0 15.8 17.8 2.3 2.4 112												•	•							
<u>1054 E5 1</u> DH65 428.8 50.4 1.2 369.7 24.0	1054	E5	1	DH65	428.8	50.4	1.2								8.6	1.9			2.7	110

Table E.1 Continued.

No.	Env.	Rep.	Name	GYLD	GPS	GWPS	SPSM	TGW	PHT	FLL	FLW	FLA	FLS	SL	SSN	FSN	TSN SC	GSP	HD
1055	E5	1	DH66	382.9	47.7		321.8	24.4						8.1	3.1	18.4	21.5 2.6	2.6	121
1056		1	DH67	492.9	41.1		467.2			•	•			7.2	1.9		17.7 2.5	2.6	114
1057		1	DH68	322.2	39.9		340.2				•		•	7.6	2.0		17.6 2.3	2.5	115
1058		1		468.5	47.4		463.0		•		•		•	7.1	1.5		17.3 2.5	3.0	113
1059		1		554.6	47.3		411.7	27.5		•		•	•	7.7	2.8		20.1 2.6	2.7	120
1060 1061		1 1	DH71 DH72	529.4 491.2	50.5 48.9		400.4 401.0		•				·	8.5 8.1	2.1 2.7		19.9 2.3 20.1 2.5	2.8 2.8	119 118
1061		1	DH72 DH73	491.2 514.6	48.9		401.0		•			•	•	8.1 7.8	2.7		20.1 2.3 19.3 2.5	2.8 2.9	118
1062		1	DH75	730.8	43.6		543.8					•	•	7.8	1.6		17.3 2.2	2.9	110
1065		1	DH76	621.8	40.7		500.2	a a a					•	7.0	2.1		17.7 2.5	2.6	117
1065		1	DH77	632.3	39.3		513.2				•			8.6	2.8		20.0 2.3	2.3	114
1066		1	DH78	602.8	48.5		422.7	a a c						8.1	1.5		18.7 2.3	2.8	113
1067	E5	1	DH79	583.5	40.7	1.2	468.7							7.5	2.8		18.5 2.5	2.6	115
1068	E5	1	DH80	559.8	45.9	1.3	423.8	28.2						7.3	2.1	17.5	19.6 2.7	2.6	116
1069	E5	1	DH81	404.2	39.7	1.0	387.5	27.0						7.4	1.8	17.3	19.1 2.6	2.3	115
1070	E5	1	DH82	559.8	39.3	1.0	573.0	26.0						7.4	2.3	15.0	17.3 2.4	2.6	109
1071		1	DH83	678.2	35.0		560.5			•				7.1	3.9		18.0 2.6	2.4	116
1072		1	DH84	688.7	39.8		547.0			•	•			7.7	1.8		17.0 2.2	2.6	109
1073		1	DH85	606.0	40.9		501.2						•	7.3	2.6		18.2 2.5	2.6	115
1074		1	DH86	587.6	41.5		508.8				•		•	6.7	2.0		17.4 2.6	2.7	114
1075		1	DH87	485.9	51.4		380.5		•			•	•	7.3	0.9		17.8 2.4	3.0	109
1076		1	DH89	529.4	35.5		495.9	20.7	•		•	•	•	7.0	2.9		18.0 2.6	2.5	116
1077		1	DH90	481.7	38.7		414.6 349.6		•			•	•	7.5	3.0 2.7		18.7 2.5	2.4	108
1078 1079		1 1	DH91 DH92	428.5	41.9 40.0		468.8		•			•	•	7.2 7.5	2.7 1.9		18.4 2.6 17.5 2.3	2.8 2.6	115 115
1079		1	DH92 DH93	454.7	40.0 53.4		350.9		•	•	•	•	•	8.2	1.9		19.3 2.3	2.0 3.0	110
1080		1		563.2	40.3		485.9	a a a			•		•	7.6	2.6		19.3 2.5	2.5	117
1081		1	DH95	505.2	37.7		593.6				•			7.7	2.0		17.3 2.2	2.5	108
1082		1		837.8	40.1		572.7				•		•	7.2	2.2		16.3 2.3	2.8	111
1084		1	DH97	581.0	46.8		410.3							7.9	1.5		19.2 2.4	2.6	114
1085		1	DH98	545.9	50.2		389.9							8.2	1.4		16.9 2.1	3.2	107
1086	E5	1	DH99	501.6	47.7	1.2	427.3	26.5						7.3	1.9		19.3 2.6	2.7	120
1087	E5	1	DH100	534.1	48.0	1.1	472.6	25.4						7.5	3.0	17.2	$20.2 \ 2.7$	2.8	114
1088	E5	1	DH101	550.6	48.8	1.3	421.2	27.3						7.9	1.9	16.4	$18.3 \ 2.3$	3.0	114
1089		1	DH102		54.3		516.5							8.7	2.6		21.6 2.5	2.8	121
1090		1	DH103		42.5		456.2				•		•	7.8	2.4		18.8 2.4	2.6	123
1091		1	DH104		48.8		613.1		•		•		•	7.1	2.8		20.5 2.9	2.7	120
1092		1	DH105		40.3		652.5		•		•	•	•	6.7	3.0		18.3 2.7	2.6	116
1093		1	DH106		38.7		525.6		•			•	•	7.8	2.8		18.7 2.4	2.4	116
1094 1095		1 1	DH107 DH108		36.9 36.2		506.1 483.4				•	•	·	7.4 6.7	2.5 3.0		17.0 2.3 18.3 2.7	2.5 2.4	113 116
1095		1	DH108		40.2		465.4			•	•	•	•	8.2	2.9		19.4 2.4	2.4	117
1090		1	DH110		46.1		331.9		•		•			8.8	2.9		19.4 2.4	2.4	113
1098		1	DH111		48.8		328.7						•	8.8	2.2		20.0 2.3	2.7	114
1099		1	DH112		40.3		328.1							7.2	3.2		19.0 2.7	2.5	117
1100		1	DH113		39.7		442.9							6.7	2.3		16.8 2.5	2.7	115
1101	E5	1	DH114	552.5	43.6	1.2	453.2	26.2						8.1	1.5	16.7	18.2 2.3	2.6	115
1102	E5	1	DH115	494.7	39.9	1.1	447.3	29.4						7.5	2.3	15.6	17.9 2.4	2.5	115
1103	E5	1	DH116	663.2	34.7	1.1	615.2	31.5						7.0	2.8	13.7	$16.5\ 2.3$	2.5	114
1104	E5	1	DH117		40.4	1.1	484.2							7.9	1.2	15.7	16.9 2.2	2.6	113
1105		1	DH119		46.2		481.9			•				8.8	2.3		19.9 2.3	2.6	115
1106		1	DH120		38.7		605.8			•	•		•	6.6	3.2		18.3 2.8	2.6	119
1107		1	DH121		38.2		475.3				•		•	7.2	4.2		19.2 2.7	2.5	120
1108		1	DH122		48.5		472.6				•		•	7.4	1.9		19.0 2.6	2.9	120
1109		1	DH123		39.5		565.7			•	•	•	•	7.3	2.6		18.1 2.5	2.5	117
1110		1	DH124		46.1		552.2			•	•	•	•	8.2	2.7		19.4 2.4	2.8	119
$1111 \\ 1112$		1	DH125 DH126		36.4 45.4		670.5 597.6			•	•	•	•	7.0 8.2	2.9 2.0		17.7 2.5 20.0 2.5	2.5 2.5	116 119
1112		1 1	DH126 DH128		45.4 43.9		476.1			•	•	•	•	8.2 7.2	2.0 3.0		20.0 2.5 20.3 2.8	2.5 2.6	119
1113		1	DH128 DH129		43.9		503.3		•	•	•	•	•	7.2 7.5	3.0		20.5 2.8 18.8 2.5	2.6	119
1115		1	DH12)		37.4		588.3		•	•	•	•	•	7.9	2.6		18.0 2.3	2.5	115
1116		1	DH130		42.6		409.5				•		•	8.1	3.4		20.8 2.6	2.4	121
		-								•	•	•	•		···		2.0		

Table E.1 Continued.

No.	Env.	Rep.	Name	GYLD	GPS	GWPS	SPSM	TGW	PHT	FLL	FLW	FLA	FLS	SL	SSN	FSN	TSN	SC	GSP	HD
1117	E5	2	DH1	433.6	37.4	0.9	458.3	24.3			•			6.7	1.8	14.1	15.9	2.4	2.6	113
1118	E5	2	DH3	596.5		1.1	565.4							6.6			16.8			120
1119	E5	2	DH4	505.9		1.1	479.0				•			7.3	2.7		18.8	2.6		117
1120	E5	2	DH5	678.2		1.1		27.2			•			8.0	2.4			2.2		117
1121	E5	2	DH6	727.2		1.2	585.9	29.2	•	•	•	•	•	7.2	1.9	15.9		2.5	2.7	109
1122 1123	E5 E5	2 2	DH7 DH8	637.6		1.2	547.3	25.2 27.8	•	•	•	•	•	6.9	3.2 2.2		19.9 18.3			123
1123	E5 E5	2	DH8 DH9	606.0 451.0		1.3 1.1		27.8	•	•	•			7.9 7.6	2.2 3.9			2.3 2.8		116 120
1124	E5	2	DH1		38.7	1.1	458.9	34.5	•	•	•	•		8.3		15.4		2.8		1120
1125	E5	2		314.5		1.1	292.8		•	•	•	•	•	7.3	2.5		19.1			115
1120	E5	2	DH12 DH13	620.3		1.3	480.1		•			•		7.8	3.4		21.4			116
1128	E5	2	DH14			1.3	509.9							7.8	3.6		19.7			117
1129	E5	2	DH15	660.2	37.7	1.1	603.5							7.5	2.0	15.1		2.3		112
1130	E5	2	DH16	713.0	40.7	1.2	604.2	29.3						7.0	1.8	15.2	17.0	2.4	2.7	112
1131	E5	2	DH17	657.9	42.2	1.4	467.9	32.2						8.0	2.0	16.1	18.1	2.3	2.6	112
1132	E5	2	DH18	538.1	48.0	1.3	401.6	27.3						8.4	2.2	18.2	20.4	2.4	2.6	123
1133	E5	2	DH19			1.1	533.7							6.9			16.5			114
1134	E5	2	DH20			1.2	470.8	26.2						7.0	3.2		19.4	2.8		119
1135	E5	2	DH21	538.1		1.1	511.5	30.8						7.1	4.0		18.1			118
1136	E5	2	DH22	469.0		1.3	361.0	28.7			•			7.8	2.9		20.4	2.6		117
1137	E5	2	DH23	484.8		1.2	415.4	26.0	•	•	•	•		6.9			17.1			112
1138	E5	2	DH24	635.4		1.2	545.8	28.8	•	•	•	•		7.1	2.1	15.0		2.4		112
1139	E5	2	DH25			1.2	504.3			•	•			7.8			19.5			112
1140	E5	2	DH26			1.0	520.6			•	•			7.1		15.2		2.5		115
1141	E5	2	DH27 DH28	791.0 658.7		1.2	642.6		•	•	•	•	•	6.5	3.1		17.7			119 117
1142 1143	E5 E5	2 2	DH28 DH29	658.7 595.6		1.2 1.2		30.4 25.1	•	•	•	•	•	6.8	2.8 3.5	15.0	17.8	2.6		117
1145	E5 E5	2	DH29 DH30			1.2	433.3	30.2	•	•	•	•	•	7.7 7.3		15.9		2.5		117
1144	E5 E5	2	DH31			1.1	433.3 511.4		•	•	•	•		7.7		15.9		2.0		116
1145	E5	$\frac{2}{2}$	DH32			0.9	622.3			•	:	•	•	7.1	2.5		18.9			123
1147	E5	2	DH32	617.5		1.3	489.7	22.2	•	•	•	•	•	7.8	2.3		22.4	2.9	2.8	123
1148	E5	2	DH34			1.6	445.5					•		8.3			18.9			110
1149	E5	2	DH35	576.3		1.1		30.6						7.6	3.0		17.9		2.3	115
1150	E5	2		657.2		1.2	566.1	27.3						8.6	2.9			2.3		117
1151	E5	2	DH37	580.8	45.2	1.2	500.3	26.5						8.0	2.7	17.1	19.8	2.5	2.6	116
1152	E5	2	DH38	519.8	43.9	1.1	473.9	23.2						7.9	1.9	16.4	18.3	2.3	2.7	109
1153	E5	2	DH39	578.9		1.3	457.7	29.3						6.3	2.1	16.5	18.6	3.0	2.4	116
1154	E5	2	DH40	421.5	36.8	1.0	404.6	28.1						8.2	2.0	17.1	19.1	2.3	2.2	117
1155	E5	2	DH41	542.7	37.7	1.1	504.4	29.7						7.1	2.6	14.5	17.1	2.4	2.6	118
1156	E5	2		459.0		1.3	364.0							7.3	2.3		20.1			116
1157	E5	2	DH43	443.1		1.2	380.4							7.0	2.8	15.2		2.6		116
1158	E5	2	DH44			1.4	453.0				•			8.1	2.9			2.3		120
1159	E5	2	DH45	586.9		1.4	431.2				•			8.1	2.8		19.4		2.2	115
1160	E5	2	DH46	545.5		1.1	476.0		•	•	•	•		8.6	3.6			2.4	2.8	120
1161	E5	2	DH47			1.0	589.9			•	•			7.2	3.7		18.3	2.5	2.6	119
1162	E5	2 2	DH49			1.3	472.7				•			7.9	3.0	16.4		2.5	2.9	120
1163	E5		DH50			1.0		31.4	•	•	•	•		7.2		14.8		2.5		116 119
1164 1165	E5 E5	2 2		548.6 585.6		1.0 1.0	538.9 600.0		•		•	•		7.6 7.1			19.3 17.6			119
1165	E5 E5	2	DH52 DH53			1.0	507.6		•	•	•	•		7.2	2.2		18.3			114
1167	E5	2		619.4		1.1	409.1		•	•	•	•	•	7.9			17.2			110
1168	E5	2		630.1		1.1	582.4		•	•	•	•	•	7.0			17.8			115
1169	E5	2		699.2		1.1	608.5			•	•	•		6.9			16.6			113
1170	E5	2		426.4		1.0	412.4							7.1			18.4			114
1171	E5	2		617.9		1.1	541.1							6.9			16.4			114
1172	E5	2		654.9		1.2	560.2							7.0			16.7			109
1173	E5	2		568.4		1.5	375.7							8.0			18.2			110
1174	E5	2		567.0		1.2	485.8	28.2						7.6			17.4		2.7	119
1175	E5	2		272.2		0.9	307.5							7.3	1.8	15.6	17.4	2.4	2.6	114
1176	E5	2		382.9		1.3	285.5							8.2			17.9			110
1177	E5	2		519.4		1.2	434.6							7.8			17.3			113
1178	E5	2	DH65	440.4	49.2	1.2	364.6	23.5			•			8.4	1.7	18.5	20.2	2.4	2.7	110

Table E.1 Continued.

No.	Env.	Rep.	Name	GYLD	GPS	GWPS	SPSM	TGW	PHT	FLL	FLW	FLA	FLS	SL	SSN	FSN	TSN SC	GSP	HD
1179	E5	2	DH66	451.0	46.5	1.3	334.4							8.0	3.5	17.9	21.4 2.7	2.6	121
1180	E5	2	DH67	540.0	41.6		447.0							7.5	2.0	16.2	18.2 2.4	2.6	114
1181		2	DH68	495.9	39.3		479.6							7.8	2.5		18.2 2.3	2.5	116
1182		2	DH69	652.6	53.3		480.2							7.3	0.9		17.4 2.4	3.2	113
1183		2	DH70	708.5	49.4		468.6							8.1	2.3		20.6 2.6	2.7	119
1184		2	DH71	620.8	47.9		477.9				•		•	8.2	2.4		19.6 2.4	2.8	119
1185 1186		2 2	DH72 DH73	485.3	43.4 44.7		420.9		•		•		•	7.5	2.9 2.6		19.2 2.6	2.6 2.7	118 118
1180		2	DH75	523.5 735.1	44.7 37.4		429.8 601.1				•		•	7.4 7.2	2.0		19.0 2.6 16.8 2.3	2.7	118
1187		2		629.2	35.5		592.5				•		•	6.9	2.2		10.8 2.5	2.0	116
1189		2	DH77	623.9	38.7		499.6				•		•	8.3	2.0		19.5 2.3	2.3	114
1190		2		717.5	43.1		561.8	a a a					•	8.0	2.2		18.5 2.3	2.6	111
1191		2		635.4	45.3		461.7							7.7	2.0		18.3 2.4	2.8	115
1192		2		549.9	45.6		425.3							7.3	1.4		18.2 2.5	2.7	116
1193	E5	2	DH81	399.8	38.1	1.1	362.5							7.5	1.8		18.4 2.5	2.3	114
1194	E5	2	DH82	507.6	39.0	1.0	487.2							7.5	1.4	15.5	16.9 2.3	2.5	108
1195	E5	2	DH83	500.6	36.6	1.3	396.0	33.5						7.2	3.6	14.2	17.8 2.5	2.6	116
1196	E5	2	DH84	532.8	32.2	1.0	511.8	32.4						7.1	2.6	13.7	16.3 2.3	2.3	108
1197	E5	2	DH85	528.8	39.7	1.2	435.6							7.5	2.3	15.8	18.1 2.4	2.5	115
1198		2	DH86	571.1	44.6		415.3							6.9	1.3		17.1 2.5	2.8	114
1199		2	DH87		41.5		412.5							7.3	1.7		17.5 2.4	2.6	108
1200		2	DH89	586.2	37.0		484.9	32.4						7.2	2.5		17.4 2.4	2.5	115
1201		2	DH90		46.9		443.1						•	7.9	2.3		18.3 2.3	2.9	108
1202		2	DH91	561.1	41.6		472.3				•		•	7.3	2.4		17.9 2.4	2.7	115
1203		2		614.1	41.6		520.4				•		•	7.5	1.5		16.8 2.3	2.7	114
1204		2	DH93	502.9	49.8		361.8				•		•	8.1	1.9		19.2 2.4	2.9	109
1205 1206		2 2	DH94 DH95	521.1 545.9	32.9 33.7		521.6				•		•	7.1 7.2	3.5 2.4		19.3 2.7	2.1 2.4	117 108
1200		2		729.9	37.3		559.9 557.6				•		•	7.1	2.4		16.5 2.3 15.9 2.2	2.4	112
1207		2		581.0	41.0		472.3						•	7.4	2.1		18.1 2.4	2.7	112
1208		2	DH98	551.8	46.1		424.8				•		•	8.1	1.3		16.9 2.1	3.0	107
1210		2	DH99		42.6		538.8		•		•		•	7.4	2.0		18.1 2.4	2.6	120
1210		2	DH100		55.2		407.6						•	7.7	1.8		19.4 2.5	3.1	113
1212		2	DH101		53.1		403.5							8.2	1.3		18.8 2.3	3.0	113
1213		2	DH102		48.0		470.5							8.3	2.9		20.8 2.5	2.7	121
1214	E5	2	DH103	487.3	36.1	1.1	441.0	30.4						7.6	3.3	15.2	18.5 2.4	2.4	123
1215	E5	2	DH104	538.1	47.8	1.4	398.0	26.0						7.2	2.6	17.8	20.4 2.9	2.7	120
1216	E5	2	DH105	527.5	36.7	1.1	465.6							6.6	3.3	14.5	17.8 2.7	2.5	116
1217	E5	2	DH106	465.9	47.0	1.2	377.4							8.3	2.2	17.6	19.8 2.4	2.7	116
1218		2	DH107		38.7		446.2							7.2	1.9		16.2 2.3	2.7	113
1219		2	DH108		37.1		484.5							7.0	2.4		18.3 2.6	2.3	116
1220		2	DH109		41.3		477.7					•		8.0	2.7		18.8 2.4	2.6	116
1221		2	DH110		47.3		389.0					•	•	9.2	2.0		20.2 2.2	2.6	113
1222		2	DH111		50.5		400.0		•		•			9.1	1.6		20.0 2.2	2.7	115
1223		2 2	DH112		37.7		447.0		•		•		•	7.3	3.1		18.9 2.6	2.4	116
1224 1225		2	DH113 DH114				440.6 516.5		•	•		•	•	6.9 7.9	2.4 2.2		17.6 2.6 18.1 2.3	2.7 2.5	115 115
1225		2	DH114 DH115				510.5			•	•	•	•	7.2	2.2		17.4 2.4	2.3	115
1220		2	DH115 DH116				592.4			•	•	•	•	7.1	2.0		16.5 2.3	2.2	113
1228		2	DH117		39.8		497.3		•	•	•	•	•	7.5	1.1		16.3 2.2	2.6	112
1220		2	DH119		40.4		516.7		•	•	•		•	8.5	3.1		19.5 2.3	2.5	115
1230		2	DH120		37.1		682.8							6.7	2.8		17.7 2.6	2.5	117
1231		2	DH121		45.6		431.8							7.9	3.9		20.8 2.6	2.7	119
1232		2	DH122		54.0		390.2							7.5	2.2		20.2 2.7	3.0	121
1233		2	DH123				428.4							7.3	2.2		18.2 2.5	2.7	117
1234	E5	2	DH124		43.1	1.2	461.0							8.0	2.8		18.8 2.4	2.7	119
1235	E5	2	DH125	597.5	37.8	1.2	489.0	32.2						7.2	2.7	15.2	17.9 2.5	2.5	115
1236		2	DH126	520.0	39.4	1.1	476.2							7.6	3.3		19.6 2.6	2.4	118
1237		2	DH128		47.6		376.4			•				7.2	2.6		20.2 2.8	2.7	119
1238		2	DH129		44.4		422.2			•	•		•	7.6	2.2		18.2 2.4	2.8	115
1239		2	DH130		42.9		470.2		•	•				7.9	2.3		18.0 2.3	2.7	116
1240	EЭ	2	DH131	503.5	41.8	1.5	394.3	28.8		•	•	•		8.0	3.6	1/.1	20.7 2.6	2.4	121

ЪŤ		Gre	eenhouse 20	012			Gr	eenhouse 20	013	
Name	PHT	FLL	FLW	FLA	FLS	PHT	FLL	FLW	FLA	FLS
DH1	73.7	23.6	1.7	32.5	13.6	78	24.1	2	37.7	12.2
DH3	76.1	27	2.1	45.8	12.6	80.2	27.3	2.6	56.1	10.5
DH4	64.9	20.7	1.9	31.5	10.8	65.8	24.7	2.2	43.5	11.1
DH5	68.9	22.5	1.9	33.2	12	75.9	26.4	2.2	45.9	12.1
DH6	79	22.5	1.9	34.2	11.7	78.6	23.7	2	38.3	11.6
DH7	66.1	17	1.9	25.3	9	71.3	28.7	2.4	53.3	12.2
DH8	72.4	18.4	1.7	24.9	10.9	78.3	28.5	2.1	46.6	13.8
DH9	72.9	17.2	2	27.8	8.5	73.9	27.7	2.5	55.4	11
DH11	91.9	21.5	1.8	31.1	11.7	86.8	29.8	2.1	50.3	14
DH12	51.9	18.8	2.1	30.5	9.2	54.8	21.6	2.2	37.2	10
DH13	65.9	18	1.8	25.3	10.1	72	27.1	2	43.1	13.5
DH14	61.8	19.1	1.9	27.9	10.3	71.9	25.9	2.3	46.5	11.4
DH15	63.7 66.9	20 20.2	1.6	25.2 27.3	12.5 12	70.1 76.1	24 27	1.7 2.1	33.4 45.7	13.7 12.6
DH16 DH17	68.7	26.6	1.7 1.6		17.5	70.1 81.7	27	2.1	45.7	12.0
DH17 DH18	73.6	16.9	2	32.6 26.1	8.6	71.8	30.5	2.6	62.4	14.2
DH18 DH19	79.9	15.6	1.9	23.7	8.3	78.4	28	2.0	51.4	12
DH19 DH20	79.9	13.0	1.9	25.7 26.4	8.5 9.9	73.5	28	2.5 2.5	51.4 59	11.5
DH20 DH21	81.3	18.6	1.8	26.4	10.5	82.8	29.5	2.3	54.4	12.1
DH21 DH22	82.3	15.1	1.6	19.3	9.4	83.4	23.4	1.9	37	11.8
DH23	76.6	21.6	1.6	26.3	13.9	78.9	27.8	2	42.8	14.3
DH24	65.2	20.3	1.9	30.6	10.7	60.5	22.3	2	36.4	11
DH25	73.4	21.5	1.6	26.6	14.5	72.6	25.6	1.9	39.5	13.2
DH26	63.3	14.9	1.5	18.3	9.6	66.2	21.9	1.8	32	12.1
DH27	78.5	15.5	1.5	18.3	10.5	79	30.3	2.4	58.4	12.4
DH28	81.5	19.7	1.6	24.1	12.7	81.4	23.7	1.8	34.2	13.1
DH29	68.7	23	2.1	37.4	11.2	69.8	25.8	2.2	45.3	11.6
DH30	74.6	25.1	1.8	35.2	14.2	78.8	26.6	2.1	44.2	12.9
DH31	74.6	19.1	2.3	34.7	8.3	76.8	23.3	2.2	40.7	10.5
DH32	68.3	15.6	1.8	21.7	8.9	70.8	25.2	2.2	43.8	11.6
DH33	79.7	20.6	1.9	30.9	11	78.6	29.7	2.4	55.8	12.5
DH34	79	17	1.9	25.5	8.9	74.7	26.5	1.9	40.5	13.8
DH35	79.5	14.5	2	22.9	7.3	74.8	20.9	2.1	34.3	10.1
DH36	75	21.1	2	34.1	10.4	76.7	27.2	2.5	53.8	10.9
DH37	77	21.2	2	33.5	10.6	76.9	27.8	1.9	40.2	15.4
DH38	66	20.6	1.5	24.5	13.7	77.1	24.7	1.9	38	12.9
DH39	76.4	13.6	1.5	16.4	8.9	74.8	22.4	1.9	33.6	11.8
DH40	78.5	13.7	1.6	17	8.7	84.2	22.2	1.8	32.8	12.1
DH41	79.2	17.4	1.6	21.9	11.1	84.5	26.4	2	41.8	13.3
DH42	72.3	18.4	1.5	21.8	12.3	77.1	26.2	2.1	42.6	12.7
DH43	77.5	14.3	1.6	18.3	8.9	79	26.7	2	42.9	13.2
DH44	84.4	19.3	1.8	26.5	11	92	28.3	2.5	56.1	11.5
DH45 DH46	68.8 77.6	18.2 21.7	1.7 1.9	24.6 32.9	10.7 11.3	77.6 79.6	24.2 30.9	2.2 2.3	41.5	11.1 13.4
DH46 DH47	77.6 74	21.7	1.9	32.9 29	11.3	79.6 76.8	30.9 23.8	2.3 2.2	56.4 41.5	13.4
DH47 DH49	74 79.4	21	2	29 41.4	12.1	76.8 77.9	23.8 29.1	2.2	41.5 50.3	10.8
DH49 DH50	75	26.1	1.9	39.6	13.2	81.4	29.1	2.2	40.6	13.9
DH50 DH51	71.1	28.7	2	39.0 45.1	13.0	81.4 74.8	24.3	2.1	40.0	11.7
DH51 DH52	62.5	27.2	1.4	30.2	14.5	70.7	24.2	1.8	35.3	14.5
DH52 DH53	57.3	18.9	2	29.5	9.6	59.8	24.9	2.2	42.9	11.5
DH55 DH54	67.7	28.3	2.2	48.3	13.2	78.4	29.8	2.4	55.5	12.7
DH55	67.6	20.5	1.7	29.8	12.9	75	23.1	1.9	35.2	12.2
DH56	62.8	26	2	40.3	13.3	70.8	22.4	2	35.6	11.2
DH57	75.3	21	1.9	30.8	11.3	69.4	24	2.1	40.2	11.3
DH58	78.6	25.4	2	39	13	83.7	25.9	2	41.3	12.8
DH59	71.1	21.8	1.5	26.6	14.1	80.5	26.4	1.9	39.9	13.9
DH60	78.9	20.5	2.1	34.1	9.7	76.6	31.9	2.3	57.4	14
DH61	70.4	16.7	1.8	23.8	9.3	72.9	27	2.1	44.3	13
DH62	78.1	21.3	1.8	30.2	11.8	75.6	28.9	2.1	48.7	13.6
DH63	73.1	25.9	2.2	44.4	11.9	77.1	28.2	2.3	50.7	12.5
DH64	79.9	21.3	1.8	30.6	11.8	85.6	23.7	1.9	36.6	12.2
DH65	66.7	14.8	1.4	16.9	10.3	75.3	27.9	1.9	42.3	14.6

Table E.2 Average phenotypic data for yield contributing traits evaluated at greenhouse 2012 and 2013. Three replications in 2012 and four in 2013. Missing data is indicated by dot.

Table E.2 Continued.

		Gre	enhouse 2	012			Gre	enhouse 2	013	
Name	PHT	FLL	FLW	FLA	FLS	PHT	FLL	FLW	FLA	FLS
DH66	71.6	16.6	2	26.2	8.3	79.4	30.3	2.8	67.9	10.8
DH67	69.4	25.4	1.8	36.1	14.1	73.3	26.3	1.8	38	14.5
DH68	69.3	21.4	2.1	34.7	10.4	73.4	24	2.4	45.3	10.1
DH69	67.7	20.4	1.6	26.3	12.6	78.3	26.8	2	41.1	13.7
DH70	76.7	16.9	1.8	24	9.4	80.2	24.9	2.1	41.8	11.8
DH71 DH72	64.7 67.7	19.8 22.1	2 1.8	31.3 31	9.9 12.5	67.6 71	26.1 23.1	2.5 1.9	51.8 34.7	10.5 12.2
DH72 DH73	68.7	18.4	1.8	26.2	12.3	72.6	23.1	2.1	54.7 44.7	12.2
DH75 DH75	77.1	18	1.3	17.6	14.6	85.2	26.7	1.8	38.4	14.7
DH76	69.2	21	1.8	29.9	11.7	70.7	24.4	2	38.4	12.6
DH77	75.6	22.3	1.6	27.6	14.3	76.7	31.3	1.8	45.6	17
DH78	82.2	15.3	1.6	20.1	9.5	80.3	28.4	2	45.6	14.1
DH79	79.1	20.5	1.7	27.5	12	82	26.3	2	41.2	13.3
DH80	77.6	19.3	1.7	25.9	11.3	75.8	27.6	1.9	42.2	14.3
DH81	66.5	11.8	1.6	14.9	7.4	70	27	2.3	48.8	11.9
DH82	72.2	20.5	1.8	28.7	11.6	78.8	27	2.1	45.1	12.8
DH83	85.9	19.3	2	30.5	9.7	88.4	24.3	1.8	35.4	13.3
DH84	72.5	17.4	1.6	22.4	10.7	77.4	25	1.9	36.6	13.5
DH85	67.3	17.1	2.1	27.9	8.3	71.5	26	2.2	44.7	12
DH86	72.2	22.8	1.7	30.1	13.6	79.5	24.2	1.8	34.5	13.5
DH87	75.9	21.5	1.6	27.8	13.3	83.2	28.4	1.9	42.7	15
DH89 DH90			2.1	45	12.9	79.3 73.2	23.2 27.4	2.1 2.2	39.2 47.9	10.9 12.4
DH90 DH91	68.1 74	27.1 13.8	2.1 1.4	15.3	9.9	78.8	27.4	2.2 1.9	47.9	12.4
DH91 DH92	75.7	22.6	1.4	31.7	12.8	76.1	26.9	1.9	40.3	14.4
DH93	72.5	18.5	1.7	25.2	10.9	67.2	26.1	1.8	37.5	14.4
DH94	72.1	19	1.7	25.5	11.2	81.2	21.3	1.9	32.6	11.1
DH95	86.3	21.5	1.6	27.2	13.4	74.2	22	1.8	32.4	12
DH96	82	17.2	1.5	20.4	11.5	80	27.8	2	45	13.6
DH97	76.5	18.7	2.1	31	8.9	78.1	23.8	2.1	40.4	11.1
DH98	72.6	21.3	2.1	35.3	10.1	72.7	27.2	2.1	44.1	13.4
DH99	77.6	14	1.7	18.8	8.2	74.8	29.1	2.7	61.9	10.8
DH100	64.7	23	1.8	32.6	12.8	66.6	26.2	2	41.2	13.2
DH101	67.9	22.4	1.8	32.3	12.3	80.3	26.3	2.1	44.6	12.2
DH102	78	16.6	1.8	23.6	9.2	79.7	29.6	2.2	52.2	13.3
DH103 DH104	71.9 78.2	28.3 25.2	2.3 1.9	50.4 37.8	12.6 13.3	74.7 83	28.3 28	2.6 2.2	59 49	10.8 12.6
DH104 DH105	67.7	23.2	1.9	37.8 40.9	15.5	85 75.8	28 28.9	2.2 1.9	32.9	12.0
DH105 DH106	72.1	17.8	1.9	26.7	9.4	71.3	24.7	2.2	42.3	11.4
DH107	71.1	19.3	1.7	25.7	11.5	76.4	24.4	2	39.2	12
DH108	79.2	11	1.6	14.1	6.8	77.1	27.3	2	42.4	13.8
DH109	69.9	16	1.8	22.8	8.9	68.8	26.6	2	41.1	13.6
DH110	80.1	21.4	1.7	28.3	12.8	81.3	26.5	2	41.4	13.4
DH111	77.8	26.8	1.8	37.1	15.4	82.9	29.1	2.1	47.6	14.1
DH112	81	13.2	1.6	16.4	8.4	74.4	23.7	1.9	36.5	12.2
DH113	82.4	12.6	1.8	17.3	7.2	83.2	24.8	2.1	40.6	12
DH114	62.9	18.8	1.9	28.2	9.9	68.7	27.1	2.2	47.5	12.2
DH115	76.6	12.1	1.6	15.6	7.5	74.9	24	1.9	36.4	12.6
DH116 DH117	83.4 72	18.8 22	1.9 2.1	27.5 36.1	10.2 10.6	83.6 77.6	22.4	2.1	36.5 46	10.9 11.2
DH119	76.7	22.4	1.9	34	11.7	78.4	25.5 25.3	2.3 2.1	40	11.2
DH119 DH120	77.6	15.2	1.6	19.4	9.5	76.7	26.6	2.1	42.1	13.4
DH120 DH121	72.9	20.7	1.8	29.9	11.4	72.3	28.2	2.4	53.6	11.8
DH121 DH122	79.6	20.4	1.4	22.2	15.5	81.2	27.6	1.9	41.3	14.6
DH123	77.6	17.6	1.4	18.9	13	76.7	21.6	1.3	22.7	16.4
DH124	76.7	20.2	1.9	29.9	10.7	73.4	27.6	2.3	51.2	11.8
DH125	67.8	19.2	1.9	29.2	10.1	71.7	22.6	2	35.1	11.6
DH126	61.6	25.6	1.7	34.9	15.3	74.8	28.9	2.4	53.9	12.3
DH128	70.3	21.4	1.6	28.2	13.1	75.8	29.7	2.3	55.4	12.9
DH129	69.1	27.9	1.7	38.1	16.1	80	24.3	1.9	36.3	12.9
DH130	69.2	22.5	2	35.6	11.3	71.7	25.8	2.1	42.8	12.3
DH131	73.5	17.9	2	28.3	9	77.3	29.2	2.6	60.2	11.2

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