IDENTIFICATION OF QTL AND CANDIDATE GENES FOR PLANT DENSITY TOLERANCE IN MAIZE

BY

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DISSERTATION

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Abstract

The global population is growing and up to three billion people will be added to the population within the next 35 years. Meanwhile, the amount of arable land for agricultural production is expected to remain the same. This suggests that grain yields will need to increase on a per unit area basis if food security is to be realized for the planet. This can be done by increasing the number of plants grown per unit area while simultaneously maintaining per plant yield. This increase in plant density will cause interplant competition for nutrients, light, and water. The ability to tolerate the increased plant density will determine the plant's ability to maintain per plant yield under conditions of increased competition.

A connected population of 320 testcross hybrids was developed using lines that previously demonstrated tolerance to high plant densities for the objective of identifying quantitative trait loci (QTL) and candidate genes for plant density tolerance. Yield trials were grown at a high plant density of 116,140 plants ha^{-1} (47,000 plants per acre [ppA]), and planted in five environments over 2012 and 2013. Grain yield and a total of 33 agronomic and morphological traits were evaluated in these five environments. QTL mapping within the nine subpopulations revealed 246 QTL and genome wide association study (GWAS) identified 11 single nucleotide polymorphisms (SNPs) with significant trait associations. Positional and functional candidate genes were investigated and are discussed.

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List of Acronyms

ASI – anthesis-silking interval
B – block
bu/A – bushels per acre
DH – double haploid
E – environment
Env1 – Environment 1
Env2 – Environment 2
Env3 – Environment 3
Env4 – Environment 4
Env5 – Environment 5
FDR – false discovery rate
G – genotype
G×E – genotype by environment interaction
G×R – genotype by replication interaction
GBS – genotype-by-sequencing
GWAS – genome wide association study
H2 – broad-sense heritability
HMM – hidden Markov model
IGD – Institute for Genomic Diversity
K matrix – kinship matrix
LAI – leaf area index
LOD – logarithm of the odds
LSMeans
MAF – minor allele frequency
MINN13 – Minnesota13
NSS – non-Stiff Stalk Synthetic
ppA – plants per acre
PVP – Plant Variety Protection
Q matrix – structure matrix
QTL – quantitative trait loci
R – replication
R:FR – red:far-red
RIL – recombinant inbred line
SNPs – single nucleotide polymorphisms
SSD – single seed descent
SSS – Stiff Stalk Synthetic
σ_g^2 – genotypic variance
$\sigma_{G\times E}^2$ – genotype by environment variance

Chapter 1

Introduction to plant density tolerance

Earth's population reached seven billion people in 2011, and it is projected that another one to three billion people will be added in the next 35 years (United Nations, 2011a; United Nations, 2011b). Additionally, the flourishing middle class in developing countries is increasing meat consumption and, therefore, expanding the need for grain as a source for livestock feed (Duvick and Cassman, 1999; Edgerton, 2009; Tilman et al., 2011). Furthermore, trends concerning climate change indicate a rise in extreme weather events such as drought, flooding, and extreme heat, which inherently increase stress in agricultural systems (Boote et al., 2011; Hatfield et al., 2011; Rosenzweig et al., 2001). Despite the growing demand for grain, the economic and ecological factors involved in the developing of new agricultural land make significant enlargement of agricultural land unlikely (Hertel, 2011). Increasing grain demand, combined with limited land availability, suggest that yield will need to increase by means of producing more grain in the same land area (Tokatlidis and Koutroubas, 2004).

Increasing grain yield per unit area can be accomplished by increasing plant density (i.e. the number of plants grown on a given unit of land) while maintaining 'per-plant' yield. Achieving yield increases by improving plant density tolerance has proven to be successful (Duvick, 2005a). Typical density increased from 30,000 plants ha^{-1} (12,000 plants per acre [ppA]) in the 1930's (Duvick, 2005b) up to 76,000 plants ha^{-1} (30,450 ppA) in 2011 (USDA-NASS, 2012a). Concurrent with these increases in plant density, there has been a yield increase of 6,383.9 kg ha^{-1} (101.8 bushels per acre [bu/A]) (USDA-NASS, 2012b). Studies show that modern hybrids yield similarly to older hybrids under conditions of low plant density; however, modern hybrids yield significantly more than older hybrids under high plant density (Brekke et al., 2011a; Brekke et al., 2011b; Duvick, 2005a)(Figure 1). This suggests an increase in plant density tolerance rather than individual plant potential as the main source of yield increase (Duvick, 2005a).

Increasing plant density tolerance can be achieved by breeding at heightened plant densities. Gradually increasing plant densities have been driven by cultural practices within commercial agriculture. In order to breed for hybrids that respond well to high plant density, the

plant selection must be done under conditions of heightened plant density. Thus, as farmers more densely planted fields and increased the demand for hybrids that performed well at high plant densities, maize breeding programs mirrored this trend in their inbred nurseries to ensure that their products performed well at these higher densities (Sangoi, 2001). Breeding in these high density environments resulted in selections with better plant density tolerance (Duvick and Cassman, 1999; Tollenaar and Lee, 2002).

By breeding at high plant density, the ability to withstand higher interplant competition is improved. High plant density causes increased competition for light, water, and nutrients. As plants are increasingly crowded, shading within the canopy occurs. Additionally, the root systems of the plants are in closer proximity at higher plant densities, meaning that roots from multiple plants are now competing for the same water, and can also potentially sense increasingly close neighbors. Similarly, the same quantity of nutrients is available for an increased number of plants at high plant density, and many nutrients are accessed by the plant through mass flow. The ability to tolerate abiotic stresses is evidenced by the plant continuing to progress from vegetative to reproductive stages. Characteristics such as ear shoot development, synchronous silking, and standability are vital to the goal of maintaining per-plant yield at high plant densities. Grain yield depends to a large degree on the plant's ability to capture sunlight, convert it to sugar, and translocate sugars to the ear where they are converted to starch in the form of kernel mass.

Grain yield is a composite trait influenced by many factors. In order to maintain yield at high plant density, per-plant grain yield must be maintained. We hypothesize that five categories of traits influence plant density tolerance: photosynthetic capacity, growth response, plant architecture, source-sink relationship, and general stress tolerance. These categories influence grain yield by means of light penetration, photosynthate accumulation, and distribution of resources to the sink.

Five categories responsible for plant density tolerance

Photosynthetic capacity

Light interception through the canopy is key to maintaining high photosynthetic capacity in plants. Increased penetration of light to the canopy is responsible for increased dry matter production (Sinclair, 1998), assimilate partitioning to the ear via local availability of photoassimilates (Hammer et al., 2009), and higher photosynthetic rates responsible for reduced percent barrenness and increased efficiency, contributing toward higher grain yields (Dwyer et al., 1991; Ipsilandis and Vafias, 2005). As plants are increasingly crowded at high plant density, the canopy begins to self-shade, which results in decreased light penetration into the canopy. This lowers photosynthetic capacity, which results in decreased grain yield (Duncan, 1971; Hammer et al., 2009; Stewart et al., 2003). Therefore, in order to maintain high photosynthetic capacity under high plant density it is important to maximize light penetration into the canopy. This is especially important as light penetration through the canopy enables more photosynthesis at/near the ear leaf, which is where much of the source allocated to the sink is distributed (Wardlaw, 1990). Leaf area index (LAI), or the amount of leaf area per unit ground area, has been found to increase at high plant densities in modern hybrids, increasing the amount of leaf area available for interception of sunlight (Cox, 1996). A large LAI ratio has been found to optimize yields at high plant density in combination with very upright leaf angles, suggesting that the combination of upright leaf angle and high leaf area per unit ground area are important to maximizing light interception and photosynthetic capacity at high density (Dong and Hu, 1993). Additional photosynthetic capacity can be achieved by extending the period during which most photoassimilates are accrued (Tollenaar and Wu, 1999) in the form of delayed senescence (i.e. staygreen) (Hammer et al., 2009). Staygreen is an important trait across various plant densities, and this indicates the importance of extending the period over which light can be intercepted (Mansfield and Mumm, 2014). Staygreen is perhaps even more important in high plant density environments, where leaf senescence rates are increased over what is observed at lower plant densities (Borras et al., 2003).

The rate of canopy closure is another important factor for maintaining photosynthetic capacity. Previous work suggested that early canopy closure benefits yield by increasing photosynthetic capacity, as well as decreasing water evaporation from the soil and minimizing weed growth (Forcella et al., 1992; Karlen and Camp, 1985; Westgate et al., 1997; Williams et

al., 1965). Interestingly, recent work suggests that the opposite may be true for high plant density; that delayed canopy closure benefits yield (Mansfield and Mumm, 2014). In the same study, leaf area to produce one g of grain was found to be negatively correlated with grain yield at various densities, while total leaf area was not significantly correlated with grain yield. This suggests that ability to achieve grain yield with a lower amount of leaf area (i.e. increased efficiency in producing grain per unit leaf area) is more indicative of plant density tolerance than total leaf area.

Growth response

Growth response reflects the reaction of maize to unfavorable environmental conditions, such as shading, that are encountered at high plant density. In response to shade, biologically defined by a reduction in the red:far-red (R:FR) ratio, maize undergoes a strengthening of apical dominance and shoot extension is favored over leaf development (Fellner et al., 2006; Fellner et al., 2003; Sawers et al., 2005). This can come at the expense of reduced leaf area and leaf thickness, lowering the amount of area available for photosynthetic processes (McLaren and Smith, 1978). Shoot extension can also come at the expense of root development, where it has been found that some genotypes respond to shade conditions by reducing the root:shoot ratio, while other maintain a more consistent root:shoot ratio under the same conditions (Hébert et al., 2001). Additionally, chlorophyll production can be affected, reducing the amount of photoassimilates that can be produced within the canopy. These various growth responses, associated with shade avoidance syndrome, have a negative impact on yield (Smith and Whitelam, 1997).

The impact on yield from growth responses is largely caused by the redirection of resources toward structures to intercept additional light instead of focusing on resource allocation to the storage organs (Kebrom and Brutnell, 2007). A number of plant hormones are responsible for the shift in favoring growth for increased light interception over allocation to storage. These include auxin, gibberellins, and ethylene (Evans and Poethig, 1995; Fellner et al., 2003; Ruther and Kleier, 2005; Sarquis et al., 1991). Thinning in some density studies take place at V4, but plant density effects have been detected at V5, suggesting that interplant competition can be sensed in the early growth stages (Ciampitti et al., 2013; Frottin et al., 2006; Sangoi, 2001). As plants encounter low R:FR light ratios, resulting from interplant competition, phytohormones

trigger a lengthening effect of the shoots in order to outcompete neighboring plants for light. This results in an increase in height and decrease in stem diameter over various densities (Lashkari et al., 2011; Sangoi et al., 2002). Lower stem diameter (as opposed to upper stem diameter) has been found to be positively correlated with rows per ear (part of ear structure) at various densities, and in another study, as plant density increased, stem diameter decreased while kernels per ear decreased, though rows per ear were unaffected (Lashkari et al., 2011; Mansfield and Mumm, 2014). These results suggest that lack of hormonal response to high plant density and associated shading may help to maintain row number per ear and ear structure.

Barrenness is another major contributor to yield loss that can result from growth response. At high plant densities, plant growth rates tend to decrease, which is especially important for seed set during flowering (Gambín et al., 2006; Rossini et al., 2011). These slower growth rates have been associated with increased barrenness at high plant density (Tollenaar et al., 2006). This is likely due to the increased apical dominance as a result high plant density induced shading (Sangoi et al., 2002). The increased apical dominance favors assimilate partitioning to the shoot over the ear, resulting in increased plant barrenness (Sangoi and Salvador, 1998; Smith and Whitelam, 1997). Response to high plant density can induce plant barrenness which can be a major contributor to yield loss and can be linked with characteristics pertaining to plant architecture and source-sink relationship. Mansfield and Mumm (2014) found barrenness to be negatively correlated with grain yield as a function of growth response at various densities.

Plant architecture

Plant architecture characteristics determine light interception into the plant canopy, and are especially important at high plant density (Hammer et al., 2009; Lambert and Johnson, 1978). Increased interception of light by green plant structures is responsible for increased dry matter production on whole (Sinclair, 1998), assimilate partitioning to the ear (Hammer et al., 2009), and higher photosynthetic rates and, therefore, increased efficiency contributing toward higher grain yields (Dwyer et al., 1991). Upright leaf angle has been associated with an increase in yield from low to high densities (Lambert and Johnson, 1978). This may be due to increased photosynthetic capacity of the canopy as light is able to penetrate deeper and more evenly into the canopy (Brekke et al., 2011b; Hammer et al., 2009). Lack of light penetration into the

canopy can shade the canopy interior and ear leaf, leading to barrenness and reduced kernel set. Mansfield and Mumm (2014) found positive correlation between leaf angle and rows per ear at various densities, suggesting that upright leaf angle may allow increased light penetration into the canopy enabling the maintenance of ear structure even at high plant densities. Although as a C4 plant corn has a higher light saturation point than C3 species, at a certain light intensity the rate of photosynthesis plateaus (Forbes and Watson, 1992). Therefore, if upright leaf angle decreases maximum light intercepted to upper leaves in favor of more even light distribution to the canopy, then efficiency in light interception could be increased.

Similarly, smaller tassel size is generally thought to contribute to increased light penetration to the canopy and increases in grain yield (Duvick et al., 2004). Lambert and Johnson (1978) showed that reduced tassel branch number and full removal of the tassel after flowering had a positive effect on yield. Reducing the tassel branch number and complete tassel removal had a significant effect on hybrids with the highest level of tassel branching, but no effect on a minimally branching hybrid, suggesting that the source of the yield increase was removal of shade caused by the tassel. Even small increases in shading in high plant density scenarios can affect levels of plant barrenness and, therefore, yield (Duncan et al., 1967). The reduction of tassel size is also thought to improve assimilate partitioning to the ear, while additionally reducing shoot growth (Monneveux et al., 2006). However, Mansfield and Mumm (2014) recently found a positive correlation between tassel branch number and rows per ear, which suggests that factors involved in determining tassel branch number are influential on the similarly developing ear. This is as expected, as there are physiological similarities between the ear and tassel during the early stages of development (Cheng et al., 1983).

Source-sink relationship

Characteristics of the source-sink relationship in maize plants are responsible for carbon partitioning, which determines the supply and demand pipeline of assimilates from production to usage endpoint (Wardlaw, 1990). Sinks are typically supplied from nearby sources (Wardlaw, 1968). This is especially important in regards to high density plantings where light penetration to the ear leaf may be hindered by shading. Source availability during very early kernel development defines the sink potential (Abendroth et al., 2011). However, after sink potential is defined, co-limitation of both source availability and sink capacity occurs, and reducing source-

sink ratios can negatively affect kernel weight (Borrás et al., 2004; Gambín et al., 2006). This suggests that source availability in early development is important to establish kernel set early on, but that source availability is also important in the post-flowering period (Gambín et al., 2006).

Source-sink limitations can influence various ear components. For grain yield to be maintained under high plant density, kernel size and kernel number must remain fairly constant. The change in light interception and resulting stress associated with high plant density can interfere with source-sink relationships and negatively impact yield by affecting these ear components (Borras et al., 2003). Kernels per row, kernels per plant, and ear diameter tend to decrease as plant density increases and plants undergo stress (Baenziger and Glover, 1980; Lashkari et al., 2011; Poneleit and Egli, 1979; Sangoi et al., 2002). Kernel growth rates, size, weight, and test weight are also influenced as plant density is increased (Gambín et al., 2006; Maddonni et al., 2006; Widdicombe and Thelen, 2002). Plant density tolerance has been found to be positively associated with rows per ear, kernels per plant, individual plant yield, kernels per row, and ear width at various densities (Mansfield and Mumm, 2014).

General stress tolerance

Stress tolerance is the ability of a plant to express its yield potential despite stresses, either biotic or abiotic (Tollenaar and Wu, 1999). Biotic stresses include insect damage, competition from weeds, or establishment of disease, whereas abiotic stresses include drought or heat stress, flooding, nutrient deficiency, or wind damage, among others. Stress tolerance can translate to yield stability, which is the ability to perform well across multiple, variable environments, and is a highly desirable attribute in crop breeding (Duvick and Cassman, 1999; Moose and Mumm, 2008; Tollenaar and Lee, 2002). Stress induced by high plant density can have similar effects to naturally occurring abiotic stresses as intense crowding can intensify competition for light, nutrients, and water and can mimic the competition experienced in normal plant density stands under certain types of environmental stresses. Furthermore, it has been shown that stress tolerances to individual abiotic stresses, such as nitrogen deficiency and drought, have "general stress tolerance" components that are applicable to a broader range of stresses (Bänziger et al., 2006; Haegele, 2012).

Increased general stress tolerance is exhibited by the plant's ability to successfully complete its reproductive cycle. Under stress, the anthesis-silking interval (ASI) can lengthen (Edmeades and Daynard, 1979), resulting in lack of kernel set and yield loss (Bolanos and Edmeades, 1996; Brekke et al., 2011b; Tokatlidis and Koutroubas, 2004). The expanded ASI separates pollen shed and silking by a longer time period due to delay in silking, which decreases the chance for successful pollination and kernel formation (Cárcova and Otegui, 2001). Increased ASI can lead to un-pollinated kernels and poor fill length. Furthermore, stress during flowering can decrease source availability and limit sink capacity, and decreased source availability during flowering and grain fill can result in aborted kernels (Abendroth et al., 2011). Collapse of ear structure (referred to as zipper effect) can also occur as a result of paired spikelet collapse under stress (Mansfield and Mumm, 2014).

In addition to effects on flowering and ear structure maintenance, stress can impact yield through increased lodging. Lodging is typically attributed to insects, stalk diseases, or poor root structure and decreases yield by making either successful pollination or harvesting difficult. Stalk lodging occurs when the stalk breaks below the ear, whereas root lodging is when the whole plant tips from its normal stance by more than 45º. Stalk lodging and root lodging are negatively correlated with grain yield at various densities (Mansfield and Mumm, 2014; Stanger and Lauer, 2007; Widdicombe and Thelen, 2002). In response to decreased light availability, the root:shoot ratio is altered in some genotypes (Hébert et al., 2001). The variability of this trait suggests that efforts to develop genotypes with a reduced response (i.e. more stable root:shoot ratios) to shading could reduce the incidence of lodging while simultaneously improving stress resistance (Hébert et al., 2001). As specific stress tolerances include a general stress component, improving general stress tolerance will be beneficial to increasing plant density tolerance.

Dissecting genetics behind plant density tolerance

Much of the research in plant density tolerance in maize that has been done at this point focuses on only one or a few traits responsible for plant density tolerance (Carlone and Russell, 1987; Dwyer et al., 1991; Lambert and Johnson, 1978; Poneleit and Egli, 1979). Due to the complexity of plant density tolerance, and the likelihood that there are many contributing genes, a comprehensive study of all possible traits underlying plant density tolerance was desirable (Crosbie et al., 2006; Heffner et al., 2009). A study with such a broad set of data will facilitate

the observation of trait to trait interactions, which could be important to understanding plant density tolerance and determining the relationships between traits which affect plant productivity at high plant density (Xu and Crouch, 2008). To this end, an initial survey of US germplasm was conducted, in part, to determine particular heterotic groups for further evaluation in plant density tolerance research, as well as which traits in the five categories underlying grain yield were significantly associated with plant density tolerance (Mansfield and Mumm, 2014).

In this study, 12 inbreds for which Plant Variety Protection had expired (ex-PVP) were chosen based on diversity and representation in the current US maize commercial germplasm base (Johnson, 2008; Mikel and Dudley, 2006). These inbred parents were crossed in diallel fashion and all of the resulting stiff stalk synthetic (SSS) by non-stiff stalk (NSS) hybrids were evaluated at six different plant densities ranging from 47,000 plants ha^{-1} (19,000 ppA) to 133,440 plants ha^{-1} (54,000 ppA), alongside four commercial checks and the twelve parent inbreds. The trials were grown in three environments over 2010 and 2011, with 48 traits measured in the hybrids. These traits corresponded to the five categories hypothesized to underlie grain yield: photosynthetic capacity, growth response, plant architecture, source-sink relationship, and general stress tolerance.

The results of Mansfield and Mumm (2014) yielded five top performing hybrids, which significantly out-yielded all other non-check hybrids at high plant density across environments. Three SSS inbred lines (PHG39, PHJ40, and B73) and three NSS inbred lines (LH82, PHG47, and PHG84) comprised the parents of the five superior hybrids. The diversity among these inbreds was important in both creating heterozygosity in future crossing schemes as well as enabling allele testing in multiple backgrounds, and the common use of these inbreds as progenitors of current germplasm increases the relevancy of results to modern hybrids. In addition to the identification of the top performing hybrids, the initial survey found that 22 of the 48 evaluated traits were either directly or indirectly correlated with grain yield across densities and environments.

The goals of this project are to identify quantitative trait loci (QTL) and candidate genes for traits associated with plant density tolerance in maize. A connected population was created by crossing recombinant inbred lines (RIL) and double haploid lines (DH) derived from intra-heterotic group breeding crosses among the inbreds which were top performing in hybrid combination at high density, as determined by Mansfield and Mumm (2014). These hybrids

were evaluated for the traits found to be directly and indirectly correlated with plant density tolerance in the same study. Additional trait data were collected based on either prevalence in the literature, for use as covariates, or to derive the 22 traits found to be significant in Mansfield and Mumm (2014). The diversity and structure of the population will be valuable for achieving these goals, as these factors will ensure the ability to test alleles in multiple backgrounds while simultaneously increasing accuracy and being able to account for population structure in mapping analyses (Jannink and Jansen, 2001; Li et al., 2005; Rebai and Goffinet, 1993; Yu et al., 2008). QTL mapping and GWAS methods were both used in analysis to determine significant chromosomal regions associated with plant density tolerance. These methods were applied to exploit the benefits of both analysis types: whereas QTL mapping is a less conservative method (i.e. allows a higher rate of false positives), which may result in an overestimation of variance, GWAS is very conservative, making it a good choice for candidate gene analysis, but possibly increasing false negatives due to a high false positive threshold (Beavis, 1994; Lande and Thompson, 1990).

Chapter 2

Introduction to QTL and candidate gene identification for plant density tolerance in maize

Grain yield is a complex trait determined by many other underlying traits. QTL for some of these underlying traits, such as flowering time, plant height, and ear height (Veldboom et al., 1994), ASI (Buckler et al., 2009), and plant height, grain moisture, kernel weight, and grain yield (Melchinger et al., 1998), among others, have been previously identified. Complex traits such as yield, in addition to being determined by multiple traits, are likely contributed to by many genes (Crosbie et al., 2006; Heffner et al., 2009). Numerous studies have explored the impact of only one or a few of these underlying traits on grain yield at high density (Carlone and Russell, 1987; Dwyer et al., 1991; Lambert and Johnson, 1978; Poneleit and Egli, 1979). Due to the complex nature of yield and considering the importance of the various categories of traits likely to impact yield under the stress of high plant density, we have taken a comprehensive approach to explore this complex trait, as there are many possible interactions between traits underpinning grain yield (Xu and Crouch, 2008). These various traits that contribute to grain yield under the stress of high plant density will need to be simultaneously studied to determine relationships between the traits and the overall impact on plant productivity. These traits affect yield by determining light interception, hormonal responses, plant growth habit, assimilate partitioning, and overall stress tolerance. However, in addition to these traits, in environments of crowding induced stress some traits which are not normally traits vital to determining yield become much more critical in the determination of yield. For instance, ASI is a trait that becomes much more pronounced under stress, as lack of water decreases silk emergence and increases ASI (Veldboom and Lee, 1996).

Mansfield and Mumm (2014) conducted an initial plant density tolerance survey to determine which of 12 diverse inbreds contributed to plant density tolerance and at what levels. Twelve inbreds for which PVP protection had expired (ex-PVP) were selected as representative of the SSS and NSS heterotic groups, and the genetic diversity comprising the current US maize commercial germplasm base (Johnson, 2008; Mikel and Dudley, 2006). It was surprising that a comparison of these 12 inbreds with the diversity core set of Yu et al. (2008) did not find an increased proportion of fixed alleles in the 12 inbreds (Hauck et al., 2014). This suggests that these 12 inbreds are a good representation of the full diversity of maize. The twelve inbred

parents were crossed in a diallel crossing design and the 32 resulting SSS by NSS hybrids were grown at six planting densities: 47,000 plants ha^{-1} (19,000 ppA), 64,250 plants ha^{-1} (26,000 ppA), 81,540 plants ha^{-1} (33,000 ppA), 98,840 plants ha^{-1} (40,000 ppA), 116,140 plants ha^{-1} (47,000 ppA), and 133,440 plants ha^{-1} (54,000 ppA), along with four commercial checks and the twelve parental inbred lines. Three environments were grown over 2010 and 2011, and 48 agronomic and morphological traits were measured. Measured traits corresponded to the five categories hypothesized to underlie grain yield: photosynthetic capacity, growth response, plant architecture, source-sink relationship, and general stress tolerance.

Out of the 48 measured traits, 16 were found to be significantly correlated with grain yield across plant densities, while an additional six traits were found to be indirectly correlated with grain yield. Days to canopy closure, individual plant yield, kernel length, kernels per plant, kernels per row, leaf angle, leaf number, rows per ear, staygreen, upper leaf area, upper stem diameter were positively correlated with grain yield, while ASI, leaf area to produce 1 g grain, percent barren plants, percent root lodged, zipper effect were negatively correlated with grain yield. Ear leaf area, fill length, kernel width, lower stem diameter, tassel branch number, and tassel weight were indirectly correlated with yield. These traits correlate with grain yield and components of grain yield across densities, signifying the importance of further examining these traits in relation to plant density tolerance. Additionally, total leaf area, plant height, tassel size, days to silk, ear width, kernel depth, and ear length, have all been associated with grain yield at high density (Boomsma et al., 2009; Buren et al., 1974; Carlone and Russell, 1987).

Mansfield and Mumm (2014) identified five hybrids that significantly out-yielded 27 others at high plant density across environments. Specifically, B73xPHG47, B73xLH82, PHJ40xPHG84, PHG39xPHG47, and PHG39xLH82 exhibited average yields between 12,330 kg ha^{-1} (196.6 bu/A) and 13,500 kg ha^{-1} (215.3 bu/A), respectively. Quadratic response to density was plotted for the five top yielding hybrids and, though results suggested optimal density had been reached for some hybrids in the study and further increasing density may result in yield loss, the response curves for PHG39xPHG47 and PHJ40xPHG84 suggested that optimal density had not yet been achieved at the high plant density. With response curves suggesting that optimal density had not been achieved even at 133,440 plants ha^{-1} (54,000 ppA), it is difficult to specify the upper limits of plant density tolerance. From the dramatic responses seen in the tested hybrids, it is obvious that this highly quantitative trait can be largely affected by genotype,

so it seems quite important to determine which agronomic traits contribute most to these high yielding genotypes and to truly pushing the limits of plant density tolerance.

Results indicated genetic diversity for plant density tolerance, with three SSS inbreds (PHG39, PHJ40, and B73) and three NSS inbreds (LH82, PHG47, and PHG84) identified as diverse inbreds, which were high yielding at high density in hybrid combination, for further study. This diversity enables alleles to be displayed in different backgrounds in test crosses, while high yield enables better statistical ability to detect differences. This diversity will be important for the objectives of this research, which are the identification of QTL and candidate genes for plant density tolerance. Additionally, since the ex-PVP parents are ancestors to current germplasm, results from the survey, as well as this experiment, have potential applicability to modern breeding programs.

Materials and Methods

Germplasm

A connected population of 320 hybrids, being connected through the six common grandparent inbreds, was constructed based on diverse ex-PVP inbreds identified as high yielding at high plant density in hybrid combination in Mansfield and Mumm (2014) (Table 1). These six ex-PVP lines were used to create RIL families by making each of the three possible crosses between the three SSS inbreds and also between the three NSS inbreds, and deriving recombinant inbred lines (RILs; through single seed descent [SSD]) and doubled haploids (DH). A total of 217 of these RILs and DH were produced this way, and these lines were then crossed to produce the 320 hybrid testcrosses that comprised the connected population for identifying QTL (Figure 2). RILs and DH from the three SSS crosses and RILs and DH from the three NSS crosses were crossed with one another in a scheme to balance the number of times each of the three crosses on both the SSS and NSS sides was represented in the overall population, while simultaneously maximizing the number of RIL and DH parents utilized in the crosses (Figure A 1). Due to seed constraints and comparatively fewer RILs and DH available for certain crosses, some inbreds were represented more often than others in hybrids, and the number of individuals in each of the subpopulations was not as balanced as the ideal scenario. The average number of times individual SSS RILs or DH were used was seven, and the average number of times NSS RILs or

DH were used was two (Figure 3), and the number of individuals in each subpopulation is shown in Table 2.

Experimental design

The 320 testcross hybrids were grown in an $\alpha(0, 1)$ incomplete block design (Patterson and Williams, 1976a) (Figure 4) with three replications in each of five environments. Each rep consisted of 20 blocks of 16 genotypes each, in two row plots. Genotypes were assigned to blocks randomly, ensuring that each entry appeared in the same block as any other entry no more than once throughout all five environments. Number of entries, environments, blocks, and replications were used to generate random design grids for the experimental layout using Gendex software (Nguyen, 2002; Nguyen and Williams, 1993; Patterson and Williams, 1976b). Blocks were configured as squares which were eight, two-row plots wide by two plots deep, resulting in 12.2 m by 12.2 m (40 foot by 40 foot) square blocks. Buffers consisted of at least eight rows on each side of the trial and at least one range on each end of the field and between replications within each location. The plant density chosen for this experiment was 116,000 plants ha^{-1} (47,000 ppA), consistent with one of the high planting densities used in the Mansfield and Mumm (2014) survey.

The trials were grown in five environments: Environment 1 (Env1) was planted on April 25th of 2012 in Urbana, IL; Environment 2 (Env2) was planted on May 5th of 2012 in Savoy, IL; Environment 3 (Env3) was planted on May 14th of 2013 in Urbana, IL; Environment 4 (Env4) was planted on May 15th of 2013 in Savoy, IL; Environment 5 (Env5) was planted on May 17th of 2013 in Monmouth, IL. Due to late plantings caused by the rainy planting season in 2013, there was no opportunity to stagger plantings without risking deviation from the target planting dates for the region, between April 20th and May 20th. The environments in 2012 were subject to substantial drought, and though there was late season drought in 2013, there were timely periods of rain through the flowering period. Field conditions are listed in Table A 1 and Table A 2. In all environments, soybean was the crop immediately preceding the trial, which was followed by deep tillage in the fall, and field cultivation in the early spring in preparation for the planting of the experiment.

The results of Mansfield and Mumm (2014) suggested competitiveness for light capture and utilization as an important source of plant density tolerance. To avoid possible confounding

of nutrient levels with plant density tolerance, and to assure non-limiting nutrients, high levels of fertilizer were applied to all environments. Nitrogen (N) was applied before planting as 28% urea-ammonium nitrate, at a rate of 336.4 kg ha^{-1} (300 lbs $acre^{-1}$), to all fields. Phosphorous (P) and Potassium (K) were each applied at 112 kg ha^{-1} (100 lbs $acre^{-1}$) over recommended levels as determined by soil tests performed by the University of Illinois Crop Science Research and Education Center.

Fields were treated with pre-emergence herbicides preceding seedling emergence. Weed control was especially important as to prevent possible activation of hormonal responses to increased competition and shading by weeds. Guardsman Max and Aatrex were applied to Env1 one week prior to planting; Frontier and Aatrex were applied to Env2 16 days prior to planting; Guardsman Max was applied to Env3 and Env4 on the morning of and the day before planting, respectively; Keystone and Roundup Weathermax were applied to Env5 four days after planting. With the exception of Env5, physical removal of additional weeds later in the growing season was achieved by hand hoeing weeds at all environments. Impact and atrazine were applied for post-emergence weed control in Env5. In all environments, Force insecticide was applied in furrow at planting to protect seedlings from rootworms. Additionally, seeds were treated with Maxim® Quattro and Cruiser® 5S before planting to protect against seed and soil borne diseases and insects, respectively.

All trials were planted with an Almaco Seed Pro 360 planter set at 76 cm (30 inches) row spacing, in 5.3 m (17.5 foot) long rows. Plots were overplanted by 15% to compensate for germination failure, and then thinned to the target plant density of 116,000 plants ha^{-1} (47,000 ppA). Thinning took place early during seedling growth (V1-V2) to avoid early plant growth responses to shading, which have been known to occur as early as V4-V6 (Maddonni and Otegui, 2004). Seedlings were thinned initially to remove any doubles, then additionally to obtain the target plant density while maintaining equal spacing between seedlings. Some plots did not achieve target plant density due to poor germination. Data from plots with stand counts lower than 106,000 plants ha^{-1} (43,000 ppA) were removed from analyses, and this missing data contributed to some genotypes not being represented in certain environments. Additionally, due to difficulty of seed production in 2012, certain genotypes were under-represented in 2013 environments. Due to the earliness of the thinning, some additional seedlings and suckers appeared post thinning. Plots with stand counts higher than the target plant density were retained

in the analysis as they were considered high density, and an attempt at using stand count as a covariate did not significantly affect experimental results.

Trait collection

Testcross hybrids were evaluated for grain yield and 33 agronomic and morphological traits (Table 3). Mansfield and Mumm (2014) identified 22 traits either directly or indirectly correlated with grain yield as density increased. These traits were scored the same as Mansfield and Mumm (2014), and an additional 11 traits were taken either for use as covariates, for the purpose of deriving correlated traits, or to maintain consistency with the literature. Days to canopy closure, days to anthesis, and days to silking were collected before and during flowering, respectively. All remaining trait data were collected post-flowering. Canopy closure was a qualitative rating determined by a visual evaluation of sunlight penetrating through the canopy, whereas the canopy was considered closed when 10% or less sunlight penetrated the canopy to reach the soil. Anthesis and silking dates were recorded when 50% of the plot was shedding pollen or showing silks, respectively. Plant height and ear height were recorded in centimeter and were measured on an average plant, as determined by viewing the entire plot and choosing a representative plant. Leaf angle was recorded in degrees and taken at the third node beneath the tassel on three different plants using a protractor. Ear leaf area was measured by destructively sampling the ear leaf from three plants per plot. The leaves were then kept at 9º C for no more than three days before scanning for leaf area. Leaves were scanned with a Li-Cor 3100 leaf area machine and measurements were recorded in centimeters squared. Total leaf area was then estimated using the regression model generated by Mansfield and Mumm (2014). Total leaf area was then multiplied by the plot's stand count to determine the total leaf area of the plot, and this value was then divided by grain yield to derive the leaf area required to produce one gram of grain. Lower stem diameter was measured with a Pittsburgh digital caliper at two angles (90º from each other) above the second node and upper stem diameter was measured with the digital calipers at the 3rd internode below the flag leaf. Lower stem diameter measurements were taken on five plants per plot in 2012, but were not taken in 2013 because preliminary data indicated upper stem diameter as a more significant component of plant density tolerance. Upper stem diameter data were collected on three plants in all environments. Staygreen was evaluated visually as a percentage of total dry down, where a rating of 1 was the worst staygreen, and 10

was the best. Root lodging, stalk lodging, and barrenness were taken as counts and a percentage rating was determined based on plot stand counts.

Five tassels were destructively sampled from each plot in Env1 and Env2. After data from 2012 indicated high heritability for tassel traits, only two tassels were sampled in Env3 and Env4, and tassels were not sampled in Env5. After tassels were collected and dried, central spike length was measured in centimeter, tassel weight was recorded in grams, and tassel branch number was recorded as a count. Additionally, five phenotyping ears were removed from all plots (except in Env5) to analyze ear related traits. Ears were dried and then measurements were taken: number of rows were counted and number of kernels per row were counted at the widest part of the ear; ear length and ear diameter were recorded, the zipper effect was measured as the percentage of a row that had experienced kernel collapse; grain weight was recorded after shelling to add back in to each plots' yield; kernel depth, width, and length were recorded in mm for two subsamples of 10 kernels each. The following traits were not collected for Env5: days to canopy closure, days to pollination, days to silking, ASI, tassel weight, tassel branch number, total spike length, leaf area, leaf area to produce 1 g grain, rows per ear, kernels per row, ear width, kernel length, kernel width, kernel depth, kernel size, ear length, and fill length. Fields were harvested with a Massey Ferguson 8-XP Research Plot Combine, and grain yield was collected. Test weight and moisture were obtained by means of a Dickey-John Mini GAC Grain Moisture Tester using subsamples of shelled grain collected from the combine.

Statistical analysis

The statistical analysis for the trials was based on the following model:

$$y_{ijkl} = \mu + E_i + R_{j(i)} + B_{k(ij)} + G_l + G \times E_{il} + G \times R_{jl(i)}$$

where

y_{ijkl} = response for the l^{th} hybrid within the k^{th} block within the j^{th} rep within the i^{th} environment
μ = overall mean
E_i = fixed effect of the i^{th} environment (i=1, 2, 3, 4, 5)
$R_{j(i)}$ = random effect of the j^{th} replication (j=1, 2, 3)
$B_{k(ij)}$ = random effect of the k^{th} block nested within the j^{th} replication and the i^{th} environment (k=1, 2, 3,…20)
G_l = fixed effect of the l^{th} hybrid (l=1, 2, 3,…320)
$G \times E_{il}$ = fixed interaction between the l^{th} hybrid and the i^{th} environment
$G \times R_{jl(i)}$ = random interaction between the l^{th} hybrid and the j^{th} replication nested within the i^{th} environment; pooled for Error

SAS 9.3 software (SAS-Institute, 2011) was used for statistical analyses. The UNIVARIATE procedure was used to obtain summary statistics on the raw data. The MIXED procedure was used to analyze the statistical model with the restricted maximum likelihood (REML) method, which can help account for unbalanced and missing data (Holland, 2006). Plant height and maturity (days to pollination) were both used as covariates in the analyses. Levene's test for homogeneity of variance was conducted to test for the ability to combine years in the analysis (Levene, 1960). The variances were unequal between years, and after further analysis of homogeneity of variance across environments within year, homogeneity of variance was obtained and two separate analyses, by year, were conducted and LSMeans were derived for all traits. LSMeans were also calculated for mean grain yield for subpopulations and the PDIFF option for LSMEANS in the MIXED procedure of SAS 9.3 software was utilized to determine significant differences between subpopulations for ranking purposes. The VARCOMP procedure of SAS 9.3 software was used to obtain variance components for use in calculating broad sense heritability (H^2) across all environments, which was calculated as:

$$H^2 = \frac{\sigma_g^2}{\sigma_p^2}$$

where

$$\sigma_p^2 = \sigma_g^2 + \frac{\sigma_{ge}^2}{env} + \frac{\sigma_E^2}{rep * env}$$

in accordance to Wyman and Baker (1991). The CORR procedure of SAS 9.3 software was utilized to determine correlation between the LSMeans of the agronomic trait data for each genotype.

Genotypic data

For each of the 217 RIL parents, five plants were grown in one well of an 8x4 cell-pak filled with Fafard potting mix. Plants were grown to V1 and then harvested directly above the plant crown. Tissue from the five plants were bulked and then a total of 0.09-0.10 g of tissue was sampled from leaf tips and placed into a 96-well tray. The samples were then frozen at -80 C overnight and, immediately upon removal from the freezer, two metal ball bearings were added to each sample and the sample tray was put in a SPEX SamplePrep Geno/Grinder 2000 at 500 strokes per min for 30 seconds for grinding. Immediately after grinding, samples underwent

DNA extraction. For DNA extraction Qiagen DNeasy Plant Mini Kits were used following the DNeasy Plant Handbook. One minor modification was applied: an additional 2 min dry-down centrifuge spin at 13,500 rpm after the Buffer AW wash. Due to the importance of high concentration DNA for genotype-by-sequencing (GBS), a total elution of only 100 µl was chosen. Samples were stored at -20 C for short term, while additional samples were being processed and checked for quality before bulk shipping. A total of 10% of the samples were subjected to a restriction enzyme reaction with HindIII for quality control to detect DNA quantity and level of shearing. Upon passing quality control standards, the DNA samples were shipped to the Institute for Genomic Diversity (IGD) at Cornell University. The samples then underwent GBS according to Glaubitz et al. (2014).

Genotype-by-sequencing is a genotyping system in which DNA sequencing technology is used to discover and identify single nucleotide polymorphism (SNP) markers. Adapters and barcodes were used to label all DNA samples and then samples were digested with ApeKI restriction enzyme. The DNA was sequenced at the IGD using an Illumina HiSeq2000, and was processed in a GBS build, or batch, of over 32,000 genotypes. This is important to note as GBS is a discovery platform and is increasingly powerful as the number of genotypes in the build increases. After sequencing, the raw sequence was fitted with a key file and tag file to match the sequence to the sample, and then it underwent several steps of data processing and error correction before SNP calling and finalization of the marker data file, called the hapmap file (Elshire et al., 2011).

For purposes of mapping QTL within each subpopulation, missing SNP marker data were imputed. GBS data provided an average coverage of 0.01x, and using a three state model (HomozygousA, Heterozygous, HomozygousB), hidden Markov model (HMM) was used to impute missing SNP data. After imputation, informative markers were selected for each of the nine subpopulations, in which markers were selected only if they differed between the two parents. The number of markers for each of the subpopulations ranged from 7,500 to 8,168 SNPs.

Bi-parental QTL analysis of subpopulations

Separate QTL analyses were run for each of the nine subpopulations in each environment for both the SSS and NSS. Trait averages over the three reps were used for the trait value. For

lines which were used in multiple crosses, the average values of the testcrosses with the common parent were used to reduce biases in the statistical analysis. Genotype-phenotype statistical relationships were calculated using a t-test, and false discovery rate (FDR) testing was performed. QTL with *P*-values having FDR <0.2 were considered to be reliable, with QTL intervals defined as the regions surrounding the QTL which were 90% or above the maximum R^2 at the peak of the QTL. After initial analysis identified a large quantity of QTL, additional criteria were applied to narrow down the results to a small set of the most influential QTL, which would be more manageable for candidate gene analysis. The criteria were that each of these influential QTL must: have at least 30% variance explained, and have an LOD score of greater than 3.0, and be one of the 22 traits associated with plant density tolerance in Mansfield and Mumm (2014).

Genome wide association study

TASSEL software was used for filtering markers (Bradbury et al., 2007). SNPs were filtered to markers which were missing 20% data or less and had at least a minor allele frequency (the frequency of the least common allele for a given SNP; MAF) of 0.02, as lower MAFs may not be distinguishable from sequencing errors (Lu et al., 2013). Marker filtering resulted in a final marker set of 2,320 SNP markers. A kinship matrix (K matrix) was calculated by GAPIT software using the VanRaden method, which is a molecular marker based method for determining kinship using marker state and allelic frequencies (VanRaden, 2008). Models accounting for population structure were fitted using both a structure matrix (Q matrix) calculated using STRUCTURE software (Pritchard et al., 2000) and GAPIT's principal component function to verify known population structure. The principal components were visualized using the G3D procedure in SAS 9.3 software. After positively verifying the population structure, the vector containing subpopulation structure was used for the final model of population structure to avoid overfitting the model, which can be the case when calculating structure through genotype when pedigree information is readily available (Astle and Balding, 2009). Various kinship and family structure models, based on different levels of missing data and other parameters, were tested to determine the best fitting model for accounting for familial relatedness. The methods were evaluated based on the QQ-plots resulting from the GWAS analysis performed in GAPIT software (Lipka et al., 2012). SNP-trait associations in GAPIT

were determined by *F*-test and FDR testing. SNP-trait associations from the GWAS analysis are reported at the 0.05 significance level, using FDR adjusted *P*-values to determine the highest confidence SNPs for further study and candidate gene analysis (Benjamini and Hochberg, 1995).

Choosing and screening potential candidate genes for traits conferring plant density tolerance

Potential candidate genes underlying the QTL and SNPs found to significantly associate with traits during the QTL and GWAS analyses were chosen by searching for both functional and positional candidate genes (Pflieger et al., 2001). Functional candidate genes were identified by searching literature and online databases, such as the Maize Genetics and Genomics Database and qTeller, for trait related genes. Positional candidate genes to screen were identified by searching the area either encompassed by the QTL interval, as determined by QTL mapping, or checking for genes overlaying the SNPs significantly associated with traits during the GWAS analysis.

The marker set used for QTL mapping and GWAS was relatively small, compared to the original GBS data set due to a high filter for missing data (20% missing data allowed) to ensure accuracy, and loss of a large number of markers when inferring hybrids from inbred data (Figure 5). High quality data were important for determining reliable QTL and narrowing the number of regions to investigate further using candidate gene analysis. Having such a high stringency for marker filtering, as previously noted, dramatically decreased the number of markers in the SNP data sets, and simultaneously reduced the amount of data. For the purpose of narrowing down potential candidate genes within the QTL regions, some of which were rather large, SNPs from the original set of markers (pre-filter) were used to enrich the regions within the QTL intervals. Markers from the raw SNP data set were filtered for 50% missing data, and a MAF of 0.02, and adding them to the region within the QTL interval. After the enrichment step, the updated marker set was used to re-run the GWAS analysis, to determine if there were any significant markers within the originally mapped QTL intervals.

Results

Phenotypic analysis

Summary statistics were calculated for all traits and the range for each trait value and mean are included in Table 4. Grain yield across years for raw data ranged from 970 kg ha^{-1} to 18,778 kg ha^{-1}, and mean grain yield was 8,530 kg ha^{-1}. However, when environment, replication, and block were taken into consideration to account for field variability, the range narrowed to span from 4,181 kg ha^{-1} to 11,945 kg ha^{-1}. For most traits plant height, maturity, or both, contributed to variation to some extent, which was accounted for by using those two traits as covariates in the model. The mean grain yield for each of the nine subpopulations, after adjusting for field variability, ranged from 7,712 kg ha^{-1} to 10,185 kg ha^{-1}(Figure 6), and the means of some populations were significantly different from others (Table 5).

Genotypic variance (σ_g^2), genotype by environment variance ($\sigma_{G\times E}^2$), and broad sense heritability (H^2) are presented in Table 4. For days to canopy closure, leaf area to produce 1 g grain, percent root lodged and percent barren plants, there was a proportionately large amount of σ_{GxE}^2 present, leading to heritabilities of 0.45, 0.46, 0.52, and 0.59, respectively, which were lower than for the other traits. However, in general, heritability was at or above expected levels for phenotypic traits. The highest heritability was observed in traits involving tassel attributes (tassel branch number, 0.96; total spike length, 0.93; tassel weight, 0.85), flowering time (days to pollination, 0.95; days to silk, 0.95), and leaf measurements (leaf angle, 0.92; ear leaf area, 0.89).

Correlations between yield and its underlying traits were calculated by year due to significant G×E interactions. For both years 2012 and 2013, individual plant yield and leaf area to produce 1 g grain were the traits most positively and negatively correlated with grain yield, respectively (Table 6). Percent barren plants and days to pollination were negatively correlated with grain yield in both 2012 and 2013, while days to silk was significantly negatively correlated with grain yield in only 2012. Kernels per plant, kernels per row, and rows per ear were positively correlated with grain yield in both years, while ear length and fill length were only significantly correlated in 2012. Several traits, including tassel branch number, staygreen, plant height, ear height, and both stalk and root lodging, experienced significant G×E, causing a reversal of correlation between 2012 and 2013. Phenotypic correlations among all traits are listed for each year in Table A 3. The correlation matrix from 2012 phenotypic data, showing r

value and significance for all trait-trait combinations. Traits are abbreviated and follow the same order as Table 3.Table A 3 and Table A 4, showing *r* value and significance.

Genotypic analysis

GBS processing of the 217 genotyped inbreds used in the construction of the connected population, yielded an initial raw data set of 2,216,729 markers with varying levels of missing data. Hybrids were then inferred from unimputed data. After filtering, the number of SNP markers decreased significantly to 2,320 markers (Figure 5). Though the inbreds had marker data with a missing data amount typical of GBS, the high level of missing data in the hybrids was due to the need for both parents to have data at the same loci in order to have informative hybrid data. For both the inbred parents and the inferred hybrids, the number of useful markers per chromosome was consistent with chromosome length, which generally declines across chromosome 1 to chromosome 10 (Figure 7). If data were imputed, the number of SNPs would increase substantially, but due to the objective of candidate gene analysis, imputation was not pursued, as having the highest quality of data was a priority.

After filtering, the set of 2,320 SNPs had an average missing data amount of 15.6%. The average proportion of markers which were heterozygous in hybrid combination was 32.1%. The rest of the markers were either fixed across the subpopulations or had common markers between the two contributing parents. The markers were focused more towards the telomere regions that the centromere regions, similar to the marker distribution in Romay et al. (2013). The average MAF, after filtering against alleles appearing in less than 2% of genotypes (as these are indistinguishable from sequencing error), across chromosomes was 23.2%. The results from the principal component analysis were plotted to illustrate the genetic segregation of the nine subpopulations (Figure 8). The first three principal components were plotted on each axis with the 320 hybrids partitioned by color according to SSS parentage and by shape to signify NSS parentage. Each color, representing the SSS parentage, was closely clustered and well defined. The different shapes within the colors, representing the NSS parentage, was more variable, and the hybrids with LH82 and PHG47 can be seen to segregate further from the center each of the SSS clusters than their PHG47xLH82 and LH82xPHG84 counterparts. These three principal components explained 100% of the variance present in the filtered marker set of 2,320 SNPs.

QTL analysis of subpopulations

QTL mapping within each of the nine subpopulations yielded a total of 246 QTL that were determined to be reliable after FDR testing, and distribution of the QTL across chromosomes was visualized, as well as distribution within the five categories of traits (Figure 9, Figure 10). Details of the 246 QTL can be found in Table A 5. Of the 246 QTL, four QTL were detected in at least two different subpopulations, eight other QTL were detected in at least two environments, and seven additional QTL were detected over both at least two different environments and two different populations. With the FDR threshold of 0.20, the LOD scores ranged from 1.77 to 7.37, and QTL were detected in all subpopulations and environments. Criteria were imposed to select a group of high influence QTL for further study in candidate gene analysis. These criteria included at least 30% explained variance, detection in at least one B73xPHG39 subpopulation, and an LOD score of 3.0 or higher. Six QTL met or surpassed these criteria and underwent further study and candidate gene analysis (Table 7). The high influence QTL include a QTL on chromosome 2 for rows per ear, a QTL for ear height on chromosome 3, QTL for staygreen on chromosomes 4 and 9, a QTL for plant height on chromosome 6, and a QTL for ASI on chromosome 9. QTL for traits which were most highly correlated with grain yield (leaf area to produce 1 g grain, percent barren plants, kernels per plant) were observed, but did not meet the criteria for being considered high influence QTL.

GWAS analysis of SNPs contributing to plant density tolerance

The 2,320 SNP markers used for the GWAS study were distributed evenly, with spacing of about 444 kb between SNPs, on average. The distances between markers ranged between 1 bp and 26.2 Mb, with sizeable gaps mainly around centromeres, skewing the distribution towards larger distances (Figure 11). Use of appropriate kinship matrix and population structure matrix resulted in QQ plots indicating that familial relatedness had been accounted for and that results were reliable and not merely artifacts of the population structure.

A total of 11 SNPs were identified for significant SNP-trait associations at the 0.05 level after FDR testing; six SNPs were identified from the 2012 data and five SNPs were identified using the 2013 data (Table 8, Figure 12). Three of those SNPs (leaf area to produce 1 g grain in 2012, and kernel width and kernel size in 2013) were significant at the 0.01 level, but due to the high correlation between the traits kernel width and kernel size, and the detection of the same significant SNP, the latter will be considered as one and discussed as kernel size. Two SNPs

were associated with total spike length; one on chromosome 1 and one on chromosome 7. On chromosome 2, a SNP was associated with days to pollination, and on chromosome 4 two SNPs were detected to be associating with rows per ear and lower stem diameter. Two SNPs were detected on chromosome 5 associated with leaf area to produce 1 g grain and percent stalk lodging, and two SNPs associating with kernel width and kernel size were co-located at the same position on chromosome 6. Two SNPs were found on different segments of chromosome 8 that were associated with leaf area to produce 1 g grain. SNP associations were not significant when data was combined across years.

Enrichment of SNP data set and identification of significant SNPs within QTL support intervals

Enriching the areas within the detected QTL intervals resulted in an expanded marker set of 3,541 SNPs. This is an additional 1,221 markers over the marker set used for the GWAS analysis, which were distributed over approximately 150 Mbp of the genome. After performing GWAS analysis with the enriched marker set, three significant SNPs within the previously detected QTL intervals were detected. One SNP significantly associated with rows per ear was detected on chromosome 2 in the previously mapped QTL interval. Additionally, a SNP-trait association for plant height was found within the QTL interval on chromosome 4, and one for ASI was detected on chromosome 9. These results will be discussed alongside the GWAS SNPs for the candidate gene analysis.

Discussion

Traits affecting plant density tolerance

Even though a subset of the 12 ex-PVP inbreds used in Mansfield and Mumm (2014) were used to create the mapping population for this experiment, there was still a high level of variability for the collected traits seen within the population. For instance, we observed significant differences in ear structure and size, ear leaf area, and staygreen can be seen in Figure A 2. While H^2 was at or above expected levels, it should be noted that H^2 for grain yield, days to canopy closure, and leaf area to produce 1 g grain was lower than expected (R.H. Mumm, personal communication, 2014). The H^2 for grain yield in Mansfield and Mumm (2014) was 0.80, while in this study we observed H^2 of 0.66. The significant differences between the

environmental conditions observed in 2012 and 2013 caused a large estimate for the G×E effect. When variance components were estimated by year, the H^2 rose from 0.66 to 0.71 and 0.78 in 2012 and 2013, respectively, which is much closer to the 0.80 observed in Mansfield and Mumm (2014). The low H^2 observed for days to canopy closure was likely due to the drought stress experienced in 2012, where some genotypes experienced leaf rolling as a stress response (Figure A 3). This response caused a delay in canopy closure of many hybrids, which was evident when after even a light precipitation event, a disproportionate number of canopies closed. The low H^2 for leaf area to produce 1 g grain was likely due to the low H^2 for grain yield, and the fact that grain yield was used in calculating this trait.

In general, correlations between grain yield and traits found to be important to plant density by Mansfield and Mumm (2014) tended to be stronger in 2012 than in 2013. Seven traits which were significantly associated with grain yield in 2012 were not found to be associated with grain yield in 2013, and six traits associated with grain yield in 2013 were not significantly associated with grain yield in 2012. The only traits that did not show a significant relationship with grain yield in either 2012 or 2013 were tassel weight, lower stem diameter, and upper stem diameter.

Individual plant yield was highly positively correlated with grain yield, as expected since individual plant yield was derived by dividing grain yield by the stand count. Other traits that showed positive correlation with grain yield (values increased for trait as grain yield increased) included kernels per plant, kernels per row, rows per ear, ear width, test weight (2012), fill length (2012), ear length (2012), percent root lodged, and percent stalk lodged. Kernel set has previously been associated with grain yield (Andrade et al., 1999), and has also been found to be related to the plant growth rate, which can be influenced by plant density stress (Echarte and Tollenaar, 2006; Rossini et al., 2011). Kernels per plant was positively correlated with yield, while kernel size was negatively associated with yield in 2012. There was a significant tradeoff between kernels per plant and kernel size ($r = -0.57^{***}$ in 2012; $r = -0.52^{***}$ in 2013), which has been previously observed (Echarte et al., 2000). While kernel length was positively correlated with grain yield (2013), both kernel width and kernel depth were negatively associated with grain yield.

Leaf area to produce 1 g grain was highly correlated with grain yield, and the findings are similar to that of Buren et al. (1974), and Mansfield and Mumm (2014). This is an informative

trait because it captures the whole cycle of grain yield from the interception of sunlight, to the efficiency of converting that energy to the production of photoassimilates, to the ability to move those photoassimilates into the ear in the form of grain yield. Percent barrenness was negatively correlated with grain yield, similarly to Earley et al. (1966), Lambert and Johnson (1978), and Mansfield and Mumm (2014). ASI was found to be correlated in the drought year 2012, but not 2013. The ASI in 2012 ranged from -1 to 11, while the flowering dates in 2013 ranged only from 0 to 5. The much larger range in 2012, combined with likely low pollen viability from high temperatures (Schoper et al., 1987), may account for ASI having a higher impact on yield in 2012 than in the milder conditions of the 2013 environments. Days to silk and days to pollination were also negatively correlated with yield in 2012, which is interesting, considering that early maturity is usually associated with decreased grain yield in comparison to later maturing hybrids (Farnham, 2001). This could be an artifact of drought avoidance, where earlier maturing hybrids yielded better as a result of not being exposed to the drought conditions as they became more severe throughout the growing season or be more a matter of when hybrids were flowering compared to the stress in 2012.

Several of the phenotypic traits changed from negatively correlated with grain yield in one year to positively correlated with grain yield in the other year. For instance, days to pollination changed from negatively correlated with grain yield in 2012 ($r = -0.44^{***}$) to positively correlated with grain yield in 2013 ($r = 0.41^{***}$) and staygreen changed from a positive correlation in 2012 ($r = 0.25^{***}$) to a negative correlation with grain yield in 2013 ($r = -0.22^{***}$). As already discussed, G×E interactions likely contributed to these inconsistent results. Plant height and ear height were both negatively correlated with grain yield in 2012, but positively correlated with grain yield in 2013. This could be explained by the severe drought stress in 2012, if plants responded too aggressively to overcrowding in an attempt to outcompete neighboring plants for sunlight, they might not have had enough resources to put back into the ear during the grain filling period. Staygreen was negatively correlated with grain yield in 2012 and positively correlated in 2013. Delayed senescence increasing yield (the positive correlation in 2013) can be explained by the increase in the period of light interception (increasing photosynthetic capacity) translating into higher grain yield (Hammer et al., 2009; Mansfield and Mumm, 2014). Though rate of senescence has been found to increase as a result of barrenness in some genotypes, this has been observed to be genotype dependent, with barren plants

maintaining green leaf area in some genotypes (Ceppi et al., 1987; Sadras et al., 2000). The positive correlation between barrenness and staygreen (r = 0.25***) in this study seems to verify the possibility that the decreased grain yield associated with increased staygreen in 2012 could be explained by increased incidence of barren plants maintaining staygreen.

Both percent stalk lodged and percent root lodged plants were positively correlated with grain yield in 2012, but negatively correlated in 2013. Early in the growing season in 2012, drought conditions had not yet begun, and a possible explanation for these positive correlations could be that plants were not water stressed and, therefore, not spending resources on developing extensive root systems. This may have resulted in plants that were able to favorably withstand drought conditions having ears which were bigger than the plant could support, resulting in increased yield per plot, despite increased lodging. Leaf angle was positively correlated with grain yield in 2013, mirroring the findings of Mansfield and Mumm (2014). The fact that this trait was not correlated with grain yield in 2012 could be explained by the effects of the drought that year. A large number of plants in the field exhibited leaf curling resulting from drought stress, which could possibly mask the effects of leaf angle on light interception into the canopy.

QTL identified for plant density tolerance

A total of 246 QTL were identified for all traits. Due to the large QTL intervals, it is unrealistic to be able to accurately identify candidate genes within these intervals. The haplotype mapping method utilized for the QTL mapping within the nine subpopulations could be improved with higher levels of recombination in the parent RIL and DH lines and is a potential next step for this research. Of the 246 QTL identified, six of the QTL were identified as high influence for traits underlying plant density tolerance (Table 7). The smallest interval for any of the six QTL was 2.9 Mbp, while the largest interval was 20.4 Mbp. Each of these QTL appear to be located in a gene rich genomic region (Anderson et al., 2006). The QTL on the short arm of chromosome 3 was previously observed explaining 7.3%, and 11% of the phenotypic variance observed for ear height in multiple studies (Berke and Rocheford, 1995; Veldboom et al., 1994). For plant height, QTL have been mapped within the QTL interval detected in this study, explaining 7.1% and 12.5% of the phenotypic variance for plant height in Beavis et al. (1991) and Koester et al. (1993), respectively. A staygreen QTL within the detected QTL region, near *waxy1* on chromosome 9 was detected by Beavis et al. (1994), explaining 25% of the phenotypic variance for staygreen. The ASI QTL on chromosome 9 was previously detected by Khairallah

et al. (1998), accounting for 3.5% of the phenotypic variance for ASI. To the best of our knowledge, QTL for staygreen or rows per ear in similar regions to this study have not been previously identified.

For QTL mapping, nine individual QTL studies were done for the individual subpopulations. In general, the effects identified in these studies were higher than previously reported for similar QTL. Due to the small size of the individual subpopulations, it is likely that this analysis results in an overestimation of the QTL effects (Beavis, 1994; Lande and Thompson, 1990). However, though the effects may be overestimated, the presence of previously identified QTL mapping to the same regions as those found in this study suggest that these are true QTL with real effects. It should be noted that there is the possibility of two QTL appearing in the same interval by chance, but the likelihood of this will be tested for in the near future. In contrast, GWAS analysis is conservative due to the need to control for the high experimentwise error rate. This conservative nature of GWAS is good for determining the highest confidence SNPs, but this, in turn, increases the rate of false negatives, for which the QTL mapping in these nine subpopulations provided a good alternative.

GWAS analysis of the connected population

A QTL for length of tassel branching space (i.e., the distance between the bottommost and uppermost tassel branch on the central tassel spike, and a subcomponent of total spike length), measured in Westerbergh and Doebley (2002), has been detected directly overlapping position of the SNP associating with total spike length on chromosome 1, explaining 8.6% of the variance for tassel branching space in a study of wild relatives of maize. QTL in the same region (bin 2.08) as the SNP on the long arm of chromosome 2 associated with days to pollination have been previously detected, explaining 9% and 11.9% of the phenotypic variance for days to pollination (Beavis et al., 1994; Veldboom and Lee, 1996). A previously detected QTL for stem diameter at internode 8 explaining 12.9% of the phenotypic variance could possibly be a match for the lower stem diameter SNP identified on the short arm of chromosome 4 (Guingo et al., 1998).

Though QTL for kernel components have previously been detected, none were located on chromosome 6 such as we observed for kernel width and kernel size (Graham et al., 1997; Peng et al., 2011). It is likely that the SNPs associating with kernel width and kernel size are the

same, as the two traits are significantly correlated (r = 0.79***). On chromosome 7, a QTL for total spike length, explaining 10% variance, has been previously detected in bin 7.02 for total spike length (Upadyayula et al., 2006). As previously mentioned, GWAS is a conservative method for mapping SNP-trait associations due to the need to control for high experimentwise error rates. This is especially important for investigating candidate genes, where the consequences of a false positive are wasted labor and materials if candidate gene verification is initiated. However, due to the increase in false negatives resulting from high thresholds against false positives, it has been suggested that the top 20 – 50 significant SNPs (based on FDR unadjusted *P*-values) in a study be examined for potentially useful QTL (A.E. Lipka, personal communication, 2014). Looking at this top percentage of QTLs could result in detection of SNPs that were, in reality, false negatives, but doing so would only be recommended for purposes where the consequences of a false positive would be negligible. An alternative method of achieving the same result would be to lower the threshold for significant SNPs (e.g. declare SNPs significant at FDR adjusted *P*-values of 0.1 instead of 0.05 or 0.01).

The connected population structure for mapping QTL in this study is useful in that there is an increased chance of polymorphism, the ability to observe alleles in multiple backgrounds, and the population structure is known, adding to the statistical power and accuracy of detecting QTL (Li et al., 2005; Rebai and Goffinet, 1993; Yu et al., 2008). By utilizing GWAS analysis, the full diversity of the population can be used, and the population structure can be accounted for to reduce associations caused by the underlying structural variation. It should be noted that creating and, therefore, knowing the population structure serves a purpose. Population structure can occur either through historic recombination or as a result of population design (McMullen et al., 2009; Tian et al., 2011). This structure can confound mapping analyses and result in the detection of false associations (Kump et al., 2011; McMullen et al., 2009; Tian et al., 2011). By knowing the structure of this population, it is possible to use the pedigree information as part of the GWAS model to account for the structure, whereas unknown structure would necessitate its estimation, which could lead to overfitting the model and possibly obscuring important results. The SNP-trait associations detected in this study are high confidence because of a high threshold against type I error. This is reflected in the relatively low number of SNPs significantly associated with traits, considering over 30 traits were evaluated, and that trait heritabilities were high.

Candidate gene analysis

Three SNPs were detected as significantly associating with rows per ear, plant height, and ASI after GWAS was performed using the enriched marker set on the QTL intervals detected in the QTL mapping of the subpopulations (Table 9). The SNP found to be associated with rows per ear within the QTL interval detected on chromosome 2 was located in a region where no genes have been previously detected. The SNP on chromosome 9 for ASI was found within the boundaries of a gene which had been detected, but whose function is unknown as of yet. Tissues in which this protein have been detected include the developing ear and seed, developing leaves, and leaf primordia, among others (Bolduc et al., 2012; Davidson et al., 2011; Li et al., 2010). The SNP found to be associated with plant height within the chromosome 6 QTL interval was located within a gene encoding a MADS-box DNA binding protein. MADS-box proteins have been examined and found to have effects on plant height in both maize and rice (Heuer et al., 2001; Jeon et al., 2000). This gene family has been majorly known for flower development, and has also been implicated in flowering time, which is relevant due to the close association of flowering time and phase change from vegetative to reproductive stages, and plant height, (Becker and Theißen, 2003; Irish and Nelson, 1991; Thornsberry et al., 2001).

For the SNPs detected as significant in the GWAS analysis, genes were detected at every SNP position (Table 9). One gene was detected for each of the significant SNPs, except for two genes being present at the percent stalk lodge associated SNP, and several of the genes had multiple transcripts. These genes were located in isolation from other genes, with an average of 5 kilobases present to either side of the gene where no other genes were located. For the SNP associated with percent stalk lodged, two genes overlapped the SNP. GRMZM2G161641 spans from 204,062,211 to 204,065,565, while GRMZM5G860516 spans from 204,062,531 to 204,065,334, with the prior overlapping the full region of the latter, and both of them overlapping the detected SNPs position of 204,064,923. For the genes detected near significant SNPs from the GWAS analysis, only two genes had protein or enzyme functions which had been analyzed and described in more depth than a simple canonical transcript (the generic name for a protein that is named based on the name of the encoding gene). These two genes were a gene associated with the SNP for lower stem diameter on chromosome 4 encoding the enzyme

methionine aminopeptidase, and a gene associated with the SNP for leaf area to produce 1 g grain on chromosome 8 for the enzyme 1-acylglycerol-3-phosphate O-acyltransferase.

On chromosome 4, overlapping the SNP associated with lower stem diameter, a gene encoding methionine aminopeptidase has been detected. Methionine is an amino acid which is typically the start codon of amino acids. Methionine aminopeptidase is an enzyme responsible for the terminal cleaving of methionine and has been implicated in gene regulation roles in Arabidopsis (Frottin et al., 2006; Walling, 2006). It has been additionally proposed to have a role in polar auxin transport (Walling, 2006). This enzyme's action in auxin transport could be partially responsible for the effect on lower stem diameter, as auxin has a role in cell expansion (Gardner et al., 1985).

On chromosome 8, where a SNP associated with leaf area to produce 1 g grain was detected, a gene encoding for the enzyme 1-acylglycerol-3-phosphate O-acyltransferase was detected in the sequence of B73, utilizing BACs and cDNA (Schnable et al., 2009; Soderlund et al., 2009). It has been associated with membranes in chloroplasts (Joyard and Douce, 1977; Murata and Tasaka, 1997). It has been suggested that this enzyme may be involved in electron transport processes (Wada and Murata, 2007). This could be explanatory for the trait leaf area to produce 1 g grain. If the electron transport processes are somehow altered by this enzyme to increase efficiency of conversion of sunlight to photoassimilates, this could produce the effect of decreasing the amount of leaf area required to produce a set amount of grain.

An overview of QTL and candidate gene identification for plant density tolerance

The connected population for this study utilized diverse ex-PVP inbreds as progenitors (Table 1). These ex-PVP inbreds were found to be top performing in hybrid combination at high density, so there are potential genotype by density interactions that may be absent in this population that might otherwise be present in populations with genotypes having less favorable reactions to high plant density. Additionally, the ability to have multiple progenitors and the inbred diversity likely led to representation of a more diverse allele set for QTL mapping than would be seen in more traditional bi-parental QTL mapping populations. The structure of the population allowed the testing of these diverse alleles in multiple backgrounds (Yu et al., 2008). There is also an increased chance of polymorphism when multiple diverse parents are utilized, and built-in replication within this type of structure. All of these factors contribute to increased

accuracy, precision, and statistical power for detecting QTL (Jannink and Jansen, 2001; Li et al., 2005; Rebai and Goffinet, 1993). One disadvantage to this type of population is the creation of the population. To achieve a balanced design, very careful planning must be used to achieve a balance of representation of each subpopulation, while also achieving a design that will allow a quantitative genetics analysis to enable the determination of additive, dominance, and epistatic effects, as well as determine general and specific combining abilities.

The results from the phenotypic analysis were mostly as expected from the literature. However, there were several traits with correlations that were contrasting to the results of Mansfield and Mumm (2014). There are numerous possible reasons which could explain the differing results between the two studies. The hybrids in Mansfield and Mumm (2014) excelled in the irrigated environment. Since correlations for that research were calculated across environments, this could be a reason for the differences in correlations between the two studies, since the environments for this experiment included a severe drought year (2012), as well as a year with late season drought (2013). As there was no irrigation for any of the environments in this study, drought tolerance is confounded with plant density tolerance. However, since growing conditions were fairly normal during vegetative growth and flowering in 2013, we feel that this study appropriately tested plant density tolerance. Additionally, since the trait category of general stress tolerance was proposed for several traits, it was expected that certain traits would confer stress tolerance of multiple stresses, being either, or both, plant density tolerance stress or drought stress.

Another possible explanation for these differences could reside in the fact that these hybrids were only grown at one plant density. Mansfield and Mumm (2014) calculated correlations across densities, while this experiment focused on only the high plant density of 116,000 plants ha^{-1} (47,000 ppA). Yet another possibility for the differences between these two studies could be lack of variability caused by selection of a subset of the genotypes tested in Mansfield and Mumm (2014). Correlations between traits are determined by the relationship of the variability of both tested traits, so a lack of variability in either trait could result in a drastically different correlation. After reviewing the results of this study, as well as the data from Mansfield and Mumm (2014), this seems unlikely as the range of trait data seem comparable between the two studies, and because of the presence of variability for traits observed in this study (Figure A 2).

Many of the traits found to be important to yield in plant density studies have previously been found to be important across a range of densities, indicating their importance to yield in general. (Lambert and Johnson, 1978; Lashkari et al., 2011; Mansfield and Mumm, 2014; Sangoi et al., 2002). Since trials were only conducted at high plant density, this study is undoubtedly detecting not only plant density tolerance QTL, but also QTL that are acting more generally, regardless of density. Though many QTLs and SNPs were determined for these traits underlying plant density tolerance, G×E interactions can affect how these traits influence yield in individual environments. This could also hold true for plantings of varying densities within the same environment, where it is conceivable that the same population, containing the same QTL and the same genes, could have different responses based on the different densities.

The objective of this study was to map QTL and significant SNPs with the purpose of utilizing candidate gene analysis to identify genes important to plant density tolerance in maize. We identified 246 QTL and 11 SNPs through GWAS which were associated with traits underlying plant density tolerance. Another three SNPs were detected within the QTL intervals resulting from GWAS performed with an enriched marker set. The results from the phenotypic analysis confirm the complexity of plant density tolerance, as all but three of the traits were associated with grain yield at high plant density. The number and breadth of the detected QTL and SNPs suggest that many small effect QTL are responsible for this complex trait.

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Tables

Table 1. Genetic makeup of the six inbred lines used as the founders of the connected population (Mansfield and Mumm, 2014; Mikel, 2006) and maturity based on growing degree units required to reach 50% silk.

Line	Group	Background	Pedigree	Developer	GDU
B73	SSS	Stiff Stalk	BSSS C5	Iowa State University	1570
PHG39	SSS	B14/B37 Stiff Stalk/ Maiz Amargo	PHA33GB4/PHA34CB4	Pioneer Hi-Bred International	1575
PHJ40	SSS	Broad-based B14/B37 Stiff Stalk	PHB09/PHB36	Pioneer Hi-Bred International	1320
LH82	NSS	Minnesota13	LH7/Holden Line 619	Holden Foundation Seeds	1428
PHG47	NSS	Diverse Oh43	PH041/MKSDTE C10	Pioneer Hi-Bred International	1360
PHG84	NSS	Oh07/Midland	PH595/PH848	Pioneer Hi-Bred International	1690

Table 2. The number of hybrids in each of the nine subpopulations making up the connected population of 320 hybrids.

	PHG47xPHG84	LH82xPHG47	LH82xPHG84
PHJ40xPHG39	27	39	33
B73xPHG39	51	49	50
PHJ40xB73	26	19	26

Table 3. Category, description, basis, and unit for measurement of the 33 phenotypic traits and grain yield measured in field tests. The 22 traits found to be directly or indirectly correlated to grain yield across densities in Mansfield and Mumm (2014) are starred.

Trait	Category	Basis	Description	Unit
Days to canopy closure*	Photosynthetic capacity	Whole plot	Days to maximum light interception	days
Ear leaf area*	Photosynthetic capacity	Three plants	Area of ear leaf	cm^2
Est. total leaf area	Photosynthetic capacity	Derived	Estimate of total leaf area	cm^2
Leaf area index	Photosynthetic capacity	Derived	Estimate of leaf area per unit ground area	ratio
Leaf area to produce 1 g grain*	Photosynthetic capacity	Derived	Leaf area per plot/grams of grain per plot	cm^2/g
Staygreen*	Photosynthetic capacity	Whole plot	Rated 1 being the worst, 10 being the best	rating
Leaf angle*	Plant architecture	Three plants	Measured on third leaf below flag leaf	degree
Tassel weight*	Plant architecture	Two or five plants	Weight of tassel	g
Total spike length	Plant architecture	Two or five plants	Length from the lowest branch to tip of spike	cm
Tassel branch number*	Plant architecture	Two or five plants	Number of tassel branches	count
Days to pollination	Growth response	Whole plot	Days to 50% plants shedding 10% pollen	days
Days to silk	Growth response	Whole plot	Days to 50% plants with visible silks	days
Plant height	Growth response	Whole plot	Distance from soil to node with flag leaf	cm
Ear height	Growth response	Whole plot	Distance from soil to node with ear	cm
Lower stem diameter*	Growth response	Five plants	Measured above second node; two angles	mm
Upper stem diameter*	Growth response	Three plants	Measured on third internode below flag leaf	mm
Percent barren plants*	Growth response	Whole plot	(Plants producing no ear/plant stand)*100	percent
Test weight	Source-sink relationship	Whole plot	Sample adjusted to 15.5% moisture	$kg\ m^{-3}$
Individual plant yield*	Source-sink relationship	Derived	Weight of grain per plot/plant stand	kg
Rows per ear*	Source-sink relationship	Five ears	Number of kernel rows	count
Kernels per row*	Source-sink relationship	Five ears	Number of kernels per row	count
Kernels per plant*	Source-sink relationship	Derived	Rows per ear x kernels per row	count
Ear width	Source-sink relationship	Five ears	Width from the middle of the ear	mm
Kernel length*	Source-sink relationship	10 kernels 2x	Length of 10 kernels arranged tip to crown	mm
Kernel width*	Source-sink relationship	10 kernels 2x	Length of 10 kernels arranged side by side	mm
Kernel depth	Source-sink relationship	10 kernels 2x	Length of 10 kernels stacked on edge	mm
Kernel size	Source-sink relationship	Derived	Kernel length x kernel width x kernel depth	mm^3
Anthesis-silking interval*	General stress tolerance	Derived	Days to pollination – days to silk	days
Percent stalk lodged	General stress tolerance	Whole plot	(Broken stalks/plant stand)*100	percent
Percent root lodged*	General stress tolerance	Whole plot	(Plants leaning >45/plant stand)*100	percent

Table 3. (cont.)

Trait	Category	Basis	Description	Unit
Zipper effect*	General stress tolerance	Five ears	Percentage of aborted rows	percent
Ear length	General stress tolerance	Five ears	Length of whole ear including cob	mm
Fill length*	General stress tolerance	Five ears	Length of ear with kernels present	mm
Grain yield*		Whole plot	Weight of grain per plot at 15.5% moisture	kg ha^{-1}

Table 4. Minimum and maximum values and mean of raw data, genotypic and genotype by environment variances, and broad-sense heritability (H^2) are listed for the 33 phenotypic traits and grain yield.

Trait	Category	Min	Max	Mean	σ_G^2	σ_{GxE}^2	H^2
Days to canopy closure	Photosynthetic capacity	49	75	60	0.46215	0.5937	0.45
Ear leaf area	Photosynthetic capacity	335.43	910.39	610.06	1696.2	300.5	0.89
Est. total leaf area	Photosynthetic capacity	1752.64	4756.88	3187.17	46196.1	8316.8	0.89
Leaf area index	Photosynthetic capacity	2.01	5.49	3.67	0.05	0.01	0.83
Leaf area to produce 1 g grain	Photosynthetic capacity	21.37	376.37	56.95	70.10	243.92	0.45
Staygreen	Photosynthetic capacity	1	10	4	0.73051	0.4209	0.85
Leaf angle	Plant architecture	35	78	60	18.3802	3.384	0.92
Tassel weight	Plant architecture	0.8	4.0	2.1	0.08542	0.0229	0.85
Total spike length	Plant architecture	23.2	49.2	36.0	7.20491	0.8677	0.93
Tassel branch number	Plant architecture	3	17	9	3.30979	0.1968	0.96
Days to pollination	Growth response	59	76	66	3.59148	0.3567	0.95
Days to silk	Growth response	60	81	69	5.33858	0.7079	0.95
Plant height	Growth response	125	321	207	119.977	17.542	0.84
Ear height	Growth response	65	181	104	59.2105	8.8601	0.90
Lower stem diameter	Growth response	12.69	25.20	18.40	0.56073	0.0773	0.65
Upper stem diameter	Growth response	2.21	10.89	7.31	0.13554	0.0527	0.73
Percent barren plants	Growth response	0	66.67	5.23	3.90315	8.0859	0.59
Test weight	Source-sink relationship	16.2	69.0	55.4	1.46168	2.1081	0.70
Individual plant yield	Source-sink relationship	0.002	0.161	0.074	4E-05	7E-05	0.67
Rows per ear	Source-sink relationship	8.6	22.4	15.4	1.07777	0.3035	0.85
Kernels per row	Source-sink relationship	11.0	44.8	27.4	3.99511	1.5478	0.78
Kernels per plant	Source-sink relationship	151.4	776.2	425.3	1795.2	517.82	0.80
Ear width	Source-sink relationship	31	52	42	1.96048	0.324	0.84
Kernel length	Source-sink relationship	82	137	107.6	0.1417	0.034	0.86
Kernel width	Source-sink relationship	52	92	71.9	0.12321	0.029	0.91
Kernel depth	Source-sink relationship	31	67	44.2	0.0452	0.0175	0.84
Kernel size	Source-sink relationship	198876	537197	341175	915.968	191.38	0.89

Table 4. (cont.)

Trait	Category	Min	Max	Mean	σ_G^2	σ_{GxE}^2	H^2
Anthesis-silking interval	General stress tolerance	-1	9	3	0.50808	0.4046	0.72
Percent stalk lodged	General stress tolerance	0	79	3	4.5477	7.1659	0.65
Percent root lodged	General stress tolerance	0	95	2	6.59694	20.965	0.52
Zipper effect	General stress tolerance	0	100	23	108.058	58.078	0.74
Ear length	General stress tolerance	82.0	216.0	141.0	61.5715	23.342	0.80
Fill length	General stress tolerance	62.8	187.0	118.6	48.6304	23.649	0.75
Grain yield		970	18778	8530	512029	858678	0.67

Table 5. The ranking of the mean grain yield for each of the nine subpopulations. Each letter represents a yield grouping for the subpopulations that signifies the difference in mean between the subpopulations. Grouping differences were significant at the 0.05 probability level.

Mean yield rank grouping				Subpopulation	Family LSMean
A				PHJ40xB73 X LH82xPHG47	9417 kg ha^{-1}
A	B			PHJ40xPHG39 X LH82xPHG47	9087 kg ha^{-1}
A	B			PHJ40xPHG39 X LH82xPHG84	9076 kg ha^{-1}
A	B			PHJ40xB73 X LH82xPHG84	9036 kg ha^{-1}
	B			B73xPHG39 X LH82xPHG47	8893 kg ha^{-1}
	B	C		PHJ40xB73 X PHG47xPHG84	8684 kg ha^{-1}
		C		B73xPHG39 X LH82xPHG84	8514 kg ha^{-1}
			D	PHJ40xPHG39 X PHG47xPHG84	8059 kg ha^{-1}
			D	B73xPHG39 X PHG47xPHG84	7800 kg ha^{-1}

Table 6. Phenotypic correlations between traits and grain yield for 2012 and 2013.

Trait	2012	2013
Leaf area to produce 1 g grain	-0.77***	-0.8***
Percent barren plants	-0.63***	-0.3***
Days to silk	-0.58***	0.00
Anthesis-silking interval	-0.57***	-0.02
Days to pollination	-0.43***	0.41***
Kernel depth	-0.39***	-0.13*
Kernel size	-0.33***	-0.10
Tassel branch number	-0.25***	0.27***
Staygreen	-0.24***	0.22***
Kernel width	-0.22***	-0.25***
Plant height	-0.21***	0.43***
Zipper effect	-0.18**	0.00
Ear height	-0.15**	0.46***
Days to canopy closure	-0.07	-0.32***
Ear leaf area	-0.07	0.13*
Est. total leaf area	-0.07	0.13*
Total spike length	-0.06	-0.25***
Upper stem diameter	-0.10	-0.08
Leaf area index	-0.10	0.17**
Tassel weight	-0.07	-0.11
Lower stem diameter	-0.01	NA
Kernel length	0.05	0.33***
Leaf angle	0.08	-0.30***
Percent stalk lodged	0.16**	-0.21***
Percent root lodged	0.19***	-0.14*
Ear length	0.21***	-0.01
Fill length	0.23***	0.09
Rows per ear	0.23***	0.27***
Test weight	0.27***	0.06
Ear width	0.30***	0.29***
Kernels per row	0.39***	0.14*
Kernels per plant	0.41***	0.32***
Individual plant yield	0.99***	0.96***

* Significant at the 0.05 probability level
** Significant at the 0.01 probability level
*** Significant at the 0.001 probability level
NA Trait data not collected in 2013

Table 7. Six high influence QTL identified by QTL mapping within each subpopulation. These six QTL are listed by chromosome order and values are shown for each of the environment/subpopulation combinations in which they were detected. The criteria to qualify as a high influence QTL were to be observed in at least two environments (Env.), to be observed in at least one of the three B73xPHG39 subpopulations (the three subpopulations with the largest sample size), and to have a percent variance explained (σ^2 exp.) of at least 30% in one of the environments. Chromosome (Chrom.) and peak position (Peak start and Peak end) are listed, where the QTL peak is defined as the region surrounding the peak that is at least 90% of the peak's maximum R^2 value.

Trait	Env.	Subpopulation	Chrom.	Peak start	Peak end	σ^2 exp.	LOD
Rows per ear	Env4	B73xPHG39 X PHG47xPHG84	2	189,543,976	211,522,624	0.232	1.78
Rows per ear	Env4	B73xPHG39 X LH82xPHG84	2	209,507,114	223,172,507	0.361	3.21
Rows per ear	Env2	B73xPHG39 X PHG47xPHG84	2	187,442,850	207,970,060	0.382	3.24
Ear height	Env1	B73xPHG39 X LH82xPHG47	3	26,928,916	58,722,938	0.409	3.43
Ear height	Env5	PHJ40xB73 X PHG47xPHG84	3	10,064,861	30,451,257	0.660	3.51
Staygreen	Env3	B73xPHG39 X LH82xPHG47	4	174,778,938	190,406,861	0.394	3.15
Staygreen	Env5	B73xPHG39 X PHG47xPHG84	4	180,911,155	190,376,044	0.559	3.73
Plant height	Env2	B73xPHG39 X LH82xPHG47	6	75,620,093	92,327,477	0.368	3.29
Plant height	Env2	B73xPHG39 X PHG47xPHG84	6	88,998,027	95,316,577	0.428	3.76
Plant height	Env1	B73xPHG39 X PHG47xPHG84	6	88,998,027	91,874,104	0.424	3.84
Staygreen	Env2	PHJ40xB73 X LH82xPHG47	9	23,531,001	45,379,465	0.526	3.08
Staygreen	Env5	B73xPHG39 X PHG47xPHG84	9	23,257,240	34,027,035	0.705	5.04
ASI	Env2	B73xPHG39 X PHG47xPHG84	9	150,006,975	156,437,290	0.488	3.05
ASI	Env3	PHJ40xB73 X LH82xPHG47	9	148,059,470	151,367,667	0.620	3.78

Table 8. The 11 SNPs significantly associated with traits underlying plant density tolerance listed by chromosome and position. Minor allele frequency is noted along with FDR adjusted *P*-values and the allelic effect for each SNP.

Chrom.	Position	Trait	Year	MAF	FDRAdj *P*-values	Allelic effect
1	63,032,450	Total spike length	2012	0.37	0.022	1.22 cm
2	205,904,801	Days to pollination	2012	0.40	0.030	-0.83 days
4	3,408,405	Rows per ear	2013	0.42	0.029	0.66 rows
4	26,427,004	Lower stem diameter	2012	0.30	0.048	-0.54 mm
5	199,389,829	Leaf area to produce 1 g grain	2012	0.49	0.009	5631.9 cm^2/g
5	204,064,923	Percent stalk lodged	2012	0.50	0.027	2.53 %
6	154,981,658	Kernel width	2013	0.39	0.001	1.75 mm
6	154,981,658	Kernel size	2013	0.39	0.008	13.51 mm^3
7	6,497,934	Total spike length	2012	0.21	0.022	-1.40 cm
8	20,961,499	Leaf area to produce 1 g grain	2013	0.42	0.031	1253.3 cm^2/g
8	116,118,932	Leaf area to produce 1 g grain	2013	0.25	0.031	-1571.1 cm^2/g

Table 9. Genes in the same region as SNP markers found to be significantly associated with traits underlying plant density tolerance. The genes are presented alongside their respective chromosomes, positions, and pathway information, as presented by MaizeCyc (Monaco et al., in preparation). The three SNPs above the line represent the SNPs detected using the enriched marker data within the QTL mapping intervals, while the 11 SNPs below the line represent SNPs detected in the initial GWAS analysis. Protein pathways are indicated by P, while enzymes are indicated with E.

Trait	Gene	Chrom.	Position of gene	Pathway
Rows per ear	None detected at site	2	NA	NA
Plant height	GRMZM2G139073_T01	6	84,785,892-84,790,566	P: MADS-box DNA binding
ASI	GRMZM2G040268	9	148,910,956-148,911,637	P: GRMZM2G040268
Total spike length	GRMZM2G109221	1	63,008,170-63,032,470	P: GRMZM2G109221
Days to pollination	GRMZM2G099622_T01	2	205,904,041-205,905,588	P: GRMZM2G099622_P01
Rows per ear	GRMZM2G478920	4	3,408,263-3,412,552	P: GRMZM2G478920
Lower stem diameter	GRMZM2G090010_T01	4	26,424,308-26,429,093	E: Methionine aminopeptidase
Leaf area to produce 1 g grain	GRMZM2G045154	5	199,388,784-199,391,155	P: GRMZM2G045154
Percent stalk lodged	GRMZM5G860516_T01	5	204,062,531-204,065,334	No pathway available
Percent stalk lodged	GRMZM2G161641_T01	5	204,062,211-204,065,565	P: GRMZM2G161641_P01
Kernel width/size	GRMZM2G037286	6	154,980,693-154,982,171	P: GRMZM2G037286
Total spike length	GRMZM2G087575	7	6,497,659-6,499,201	P: GRMZM2G087575
Leaf area to produce 1 g grain	GRMZM2G147840	8	20,960,400-20,962,444	P: GRMZM2G147840
Leaf area to produce 1 g grain	GRMZM2G166176	8	116,118,395-116,120,825	E: 1-acylglycerol-3-phosphate O-acyltransferase

Figures

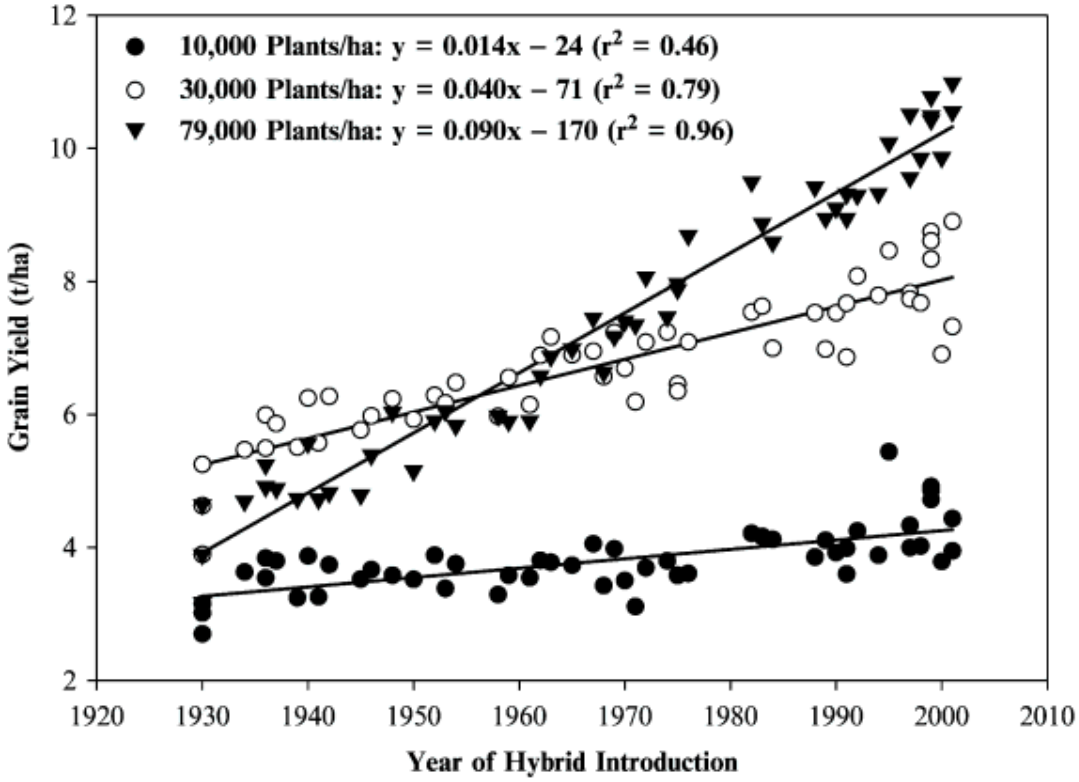


Figure 1. In an era study (Duvick, 2005b), hybrids produced in the early 2000's did not have significantly different yield potential for individual plants from hybrids produced in the 1930's. The most significant grain yield gains from the more recently produced hybrids were achieved at a comparatively significantly higher plant density.

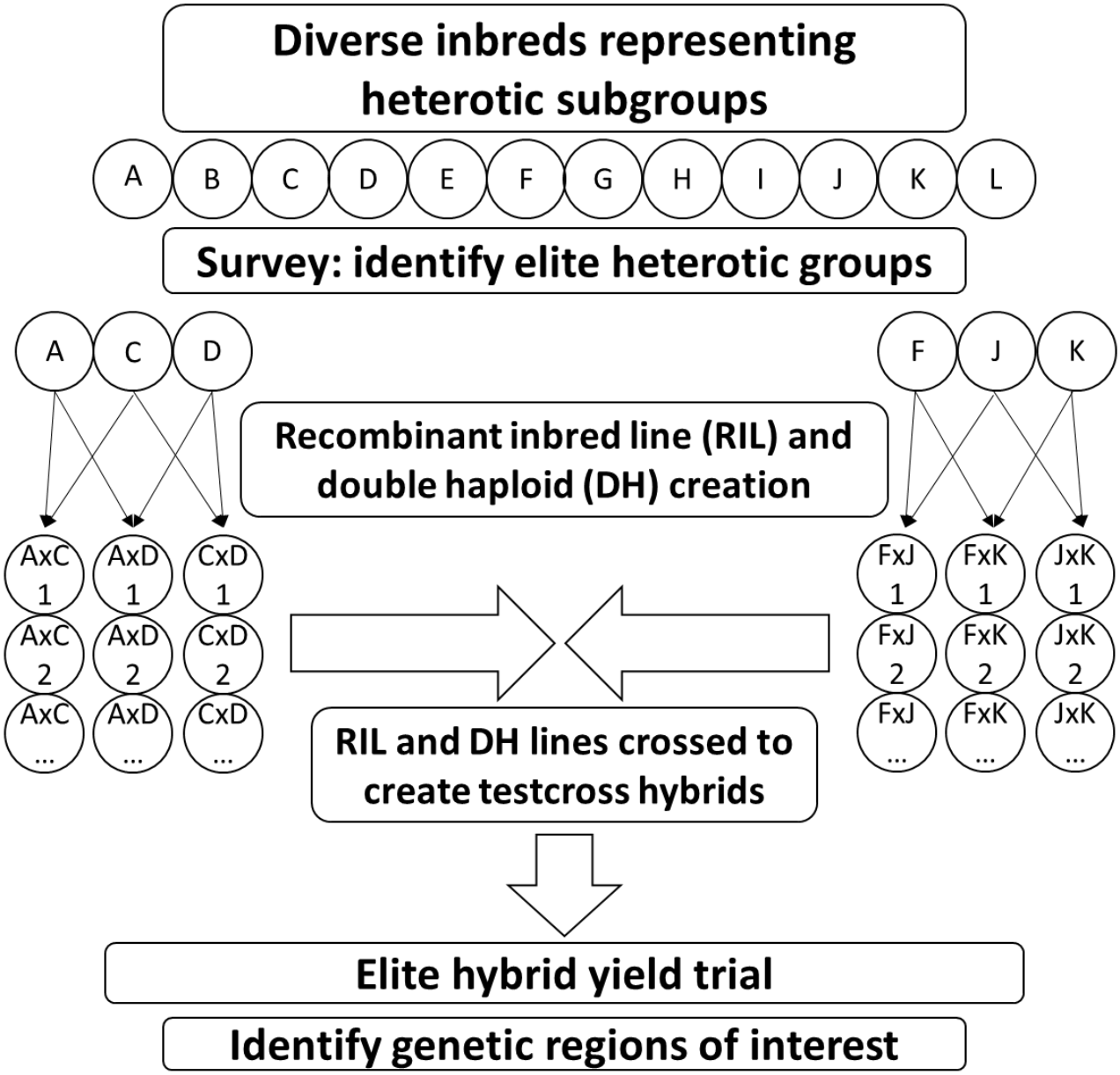


Figure 2. The connected population structure. Letters A through L represent the initial set of 12 ex-PVP inbreds in the initial plant density tolerance survey (Mansfield and Mumm, 2014). Six of these inbreds were selected as parents for the connected population based on the results of the survey. Inbreds A, C, and D represent the SSS inbreds B73, PHG39, and PHJ40, respectively, and inbreds F, J, and K represent the NSS inbreds LH82, PHG47, and PHG84, respectively. RILs and DH lines were available for each of the three possible crosses within the heterotic groups. These RILs and DH lines from the SSS and NSS families were crossed to maximize the number of RIL and DH parents used in the creation of the population, as well as maintain the balance of individuals in each of the nine resulting subpopulations.

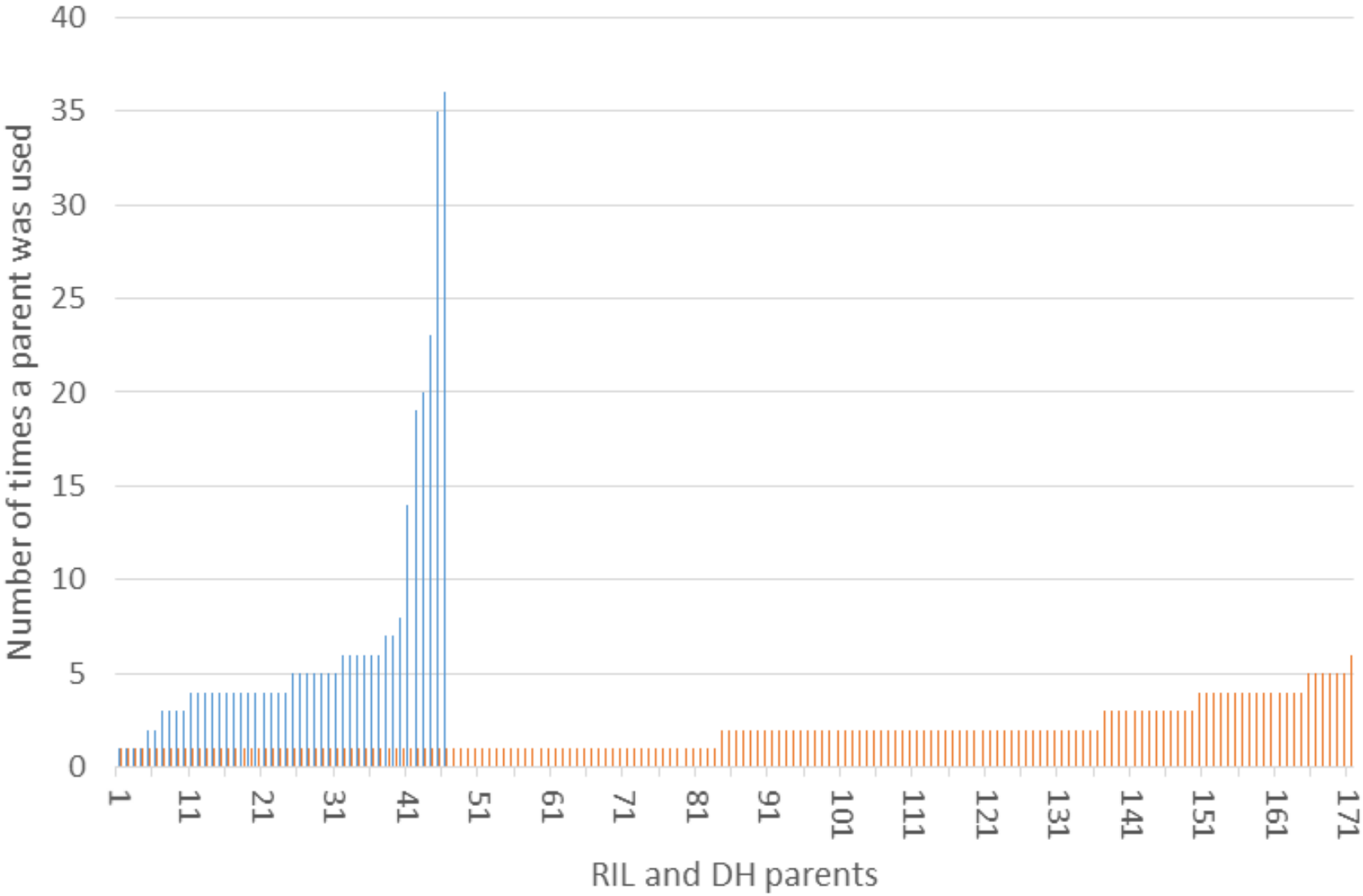


Figure 3. The 217 DH and RIL parents were used to create 320 testcross hybrids. There were fewer available SSS parents available for use, which resulted in a higher number of crosses to be made per inbred line on the SSS side of the heterotic pattern than with the NSS side. A total of 46 SSS inbreds were used and a total of 171 NSS parents were used.

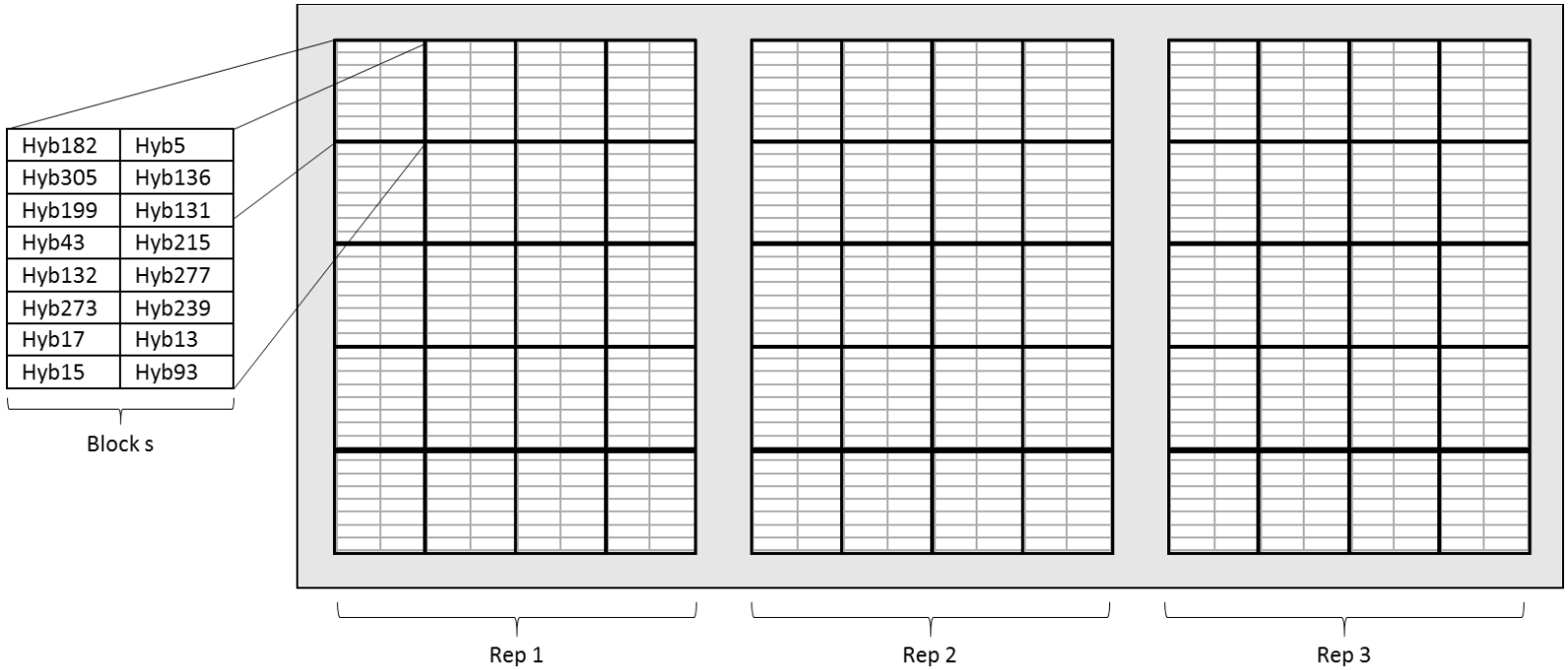


Figure 4. The α(0, 1) incomplete block design. The gray background is representative of one range of border rows in between, in front, and in back of, each replication, as well as eight rows of border to each side. Each replication contained 20 blocks consisting of 16 hybrid entries each, in an eight-plot by two-plot pattern. In the experimental model, replications were nested within environment, and blocks were nested within replication.

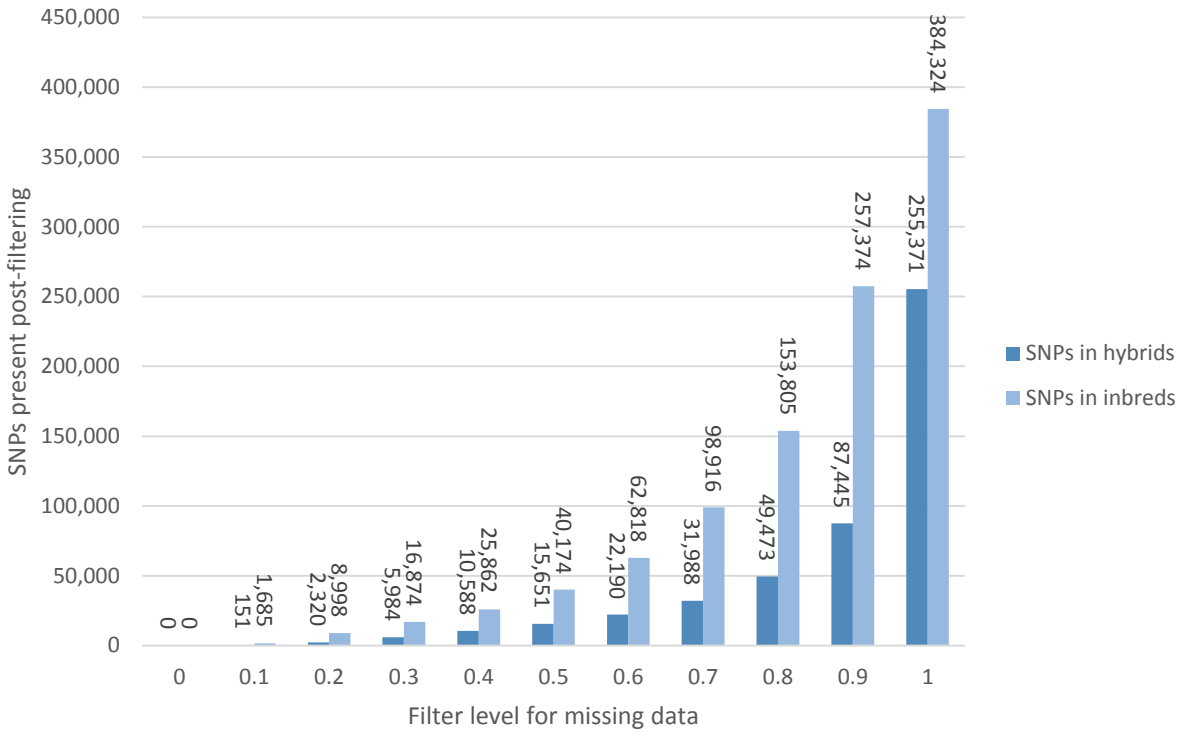


Figure 5. The number of SNPs present in the genotyped inbred parents was higher than the number of SNPs present in the inferred hybrids. These data illustrate the number of SNPs present at missing data levels from 0% to 100% missing data allowable. Markers with MAF lower than 0.02 were not included.

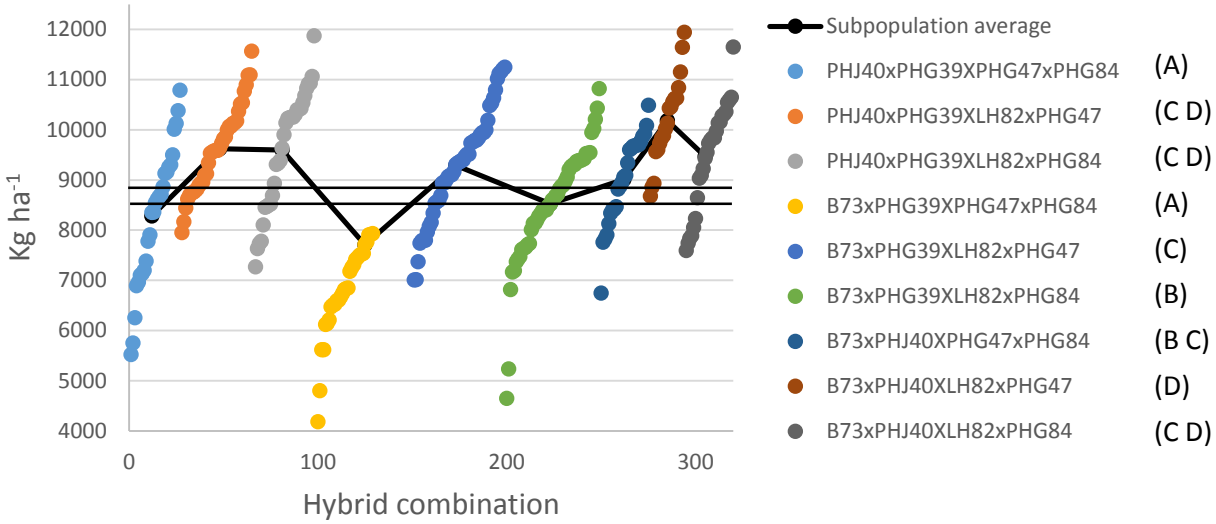


Figure 6. Grain yield of the 320 testcross hybrids. Hybrids are ranked by mean grain yield within each subpopulation, over all environments. The thin black lines represent the overall mean grain yield of 8530 kg ha^{-1} (139.5 bu/A) for the raw data, and 8948 kg ha^{-1} (142.6 bu/A) for the LSMeans, while the thick black line represents the mean grain yield for individual subpopulations. The letters to the right of each subpopulation indicate grouping according to significant differences between the mean grain yields of each subpopulation.

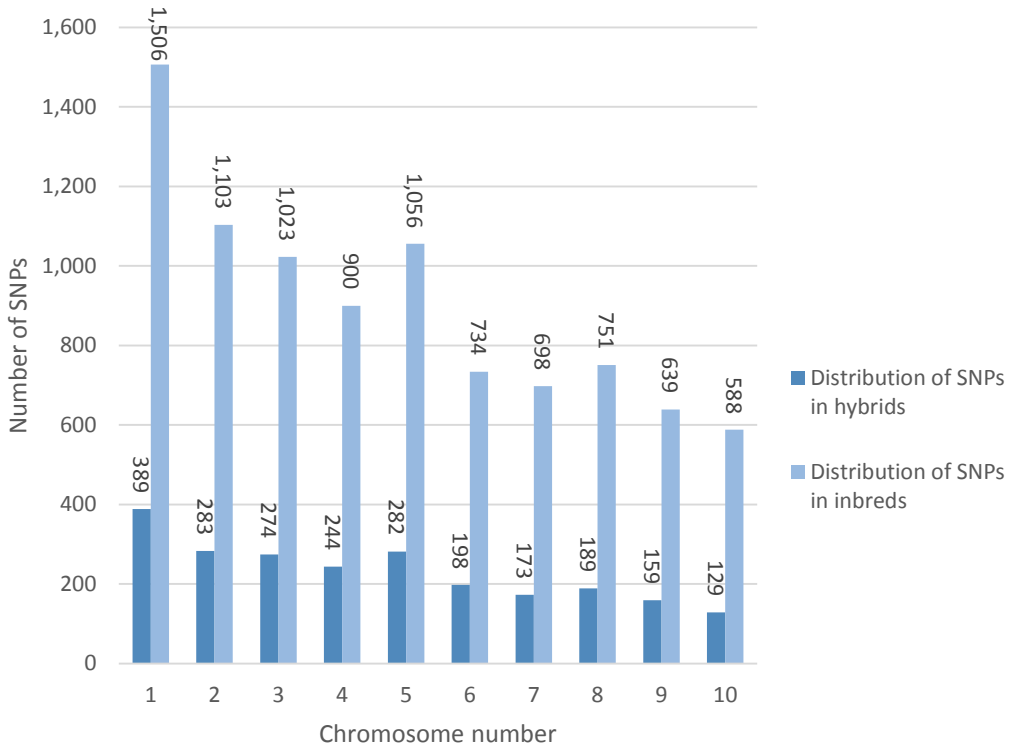


Figure 7. The marker distributions from the 217 genotyped inbreds are shown next to the distributions from the inferred hybrid genotypes. The markers are distributed among the 10 chromosomes of maize.

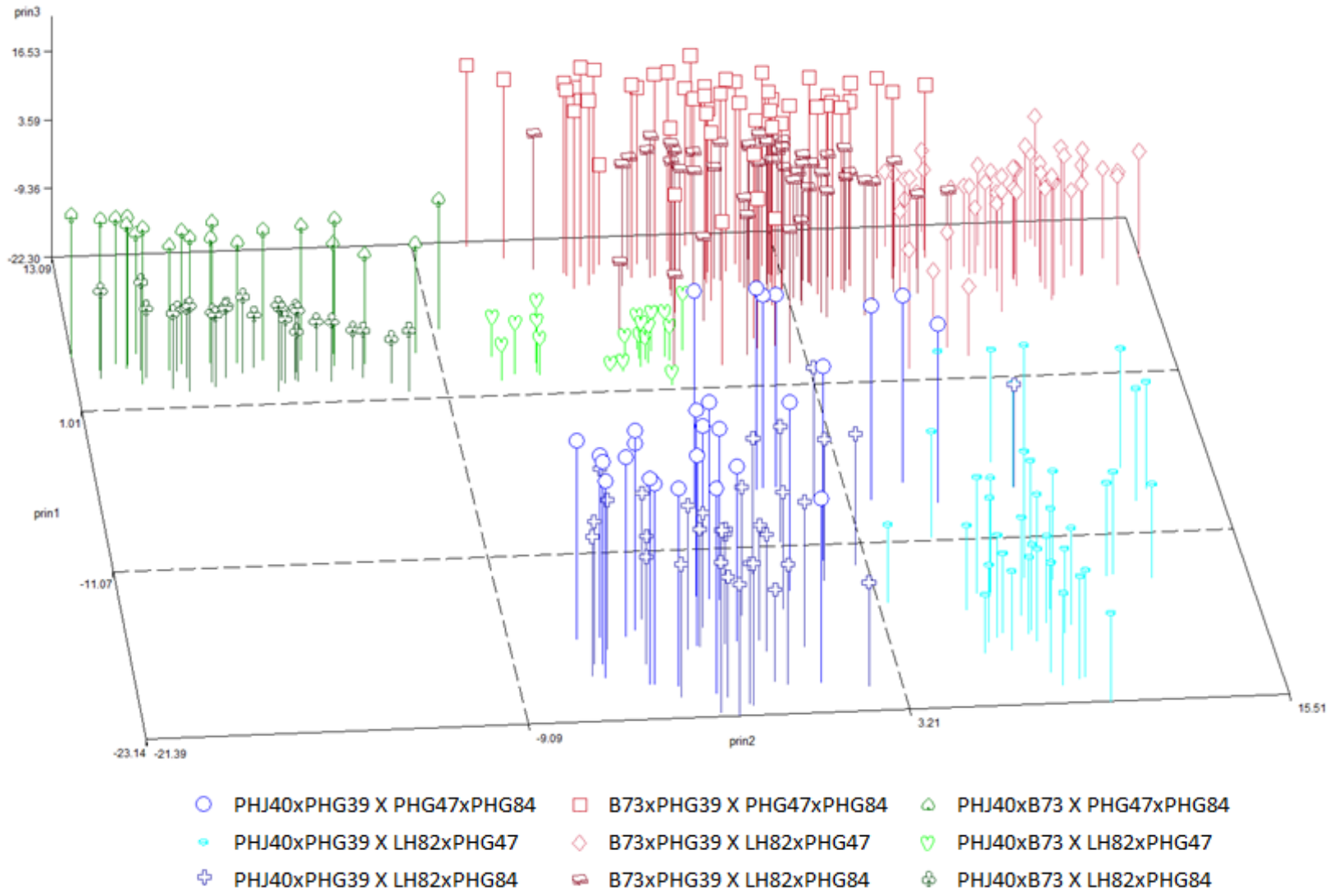


Figure 8. The nine subpopulations segregating by the first three principal components from the principal component analysis of the 2,320 SNPs analyzed using GWAS.

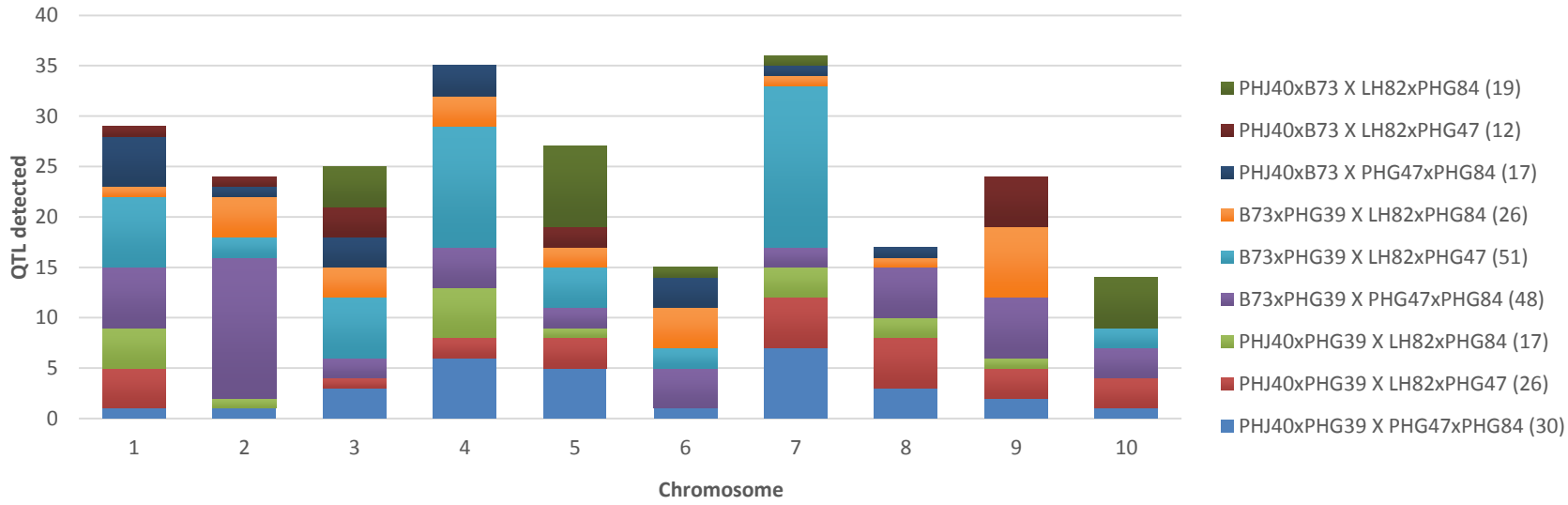


Figure 9. The distribution of detected QTL. A total of 246 QTL were determined and the number of QTL for each subpopulation is listed in parentheses behind the corresponding subpopulation in the legend.

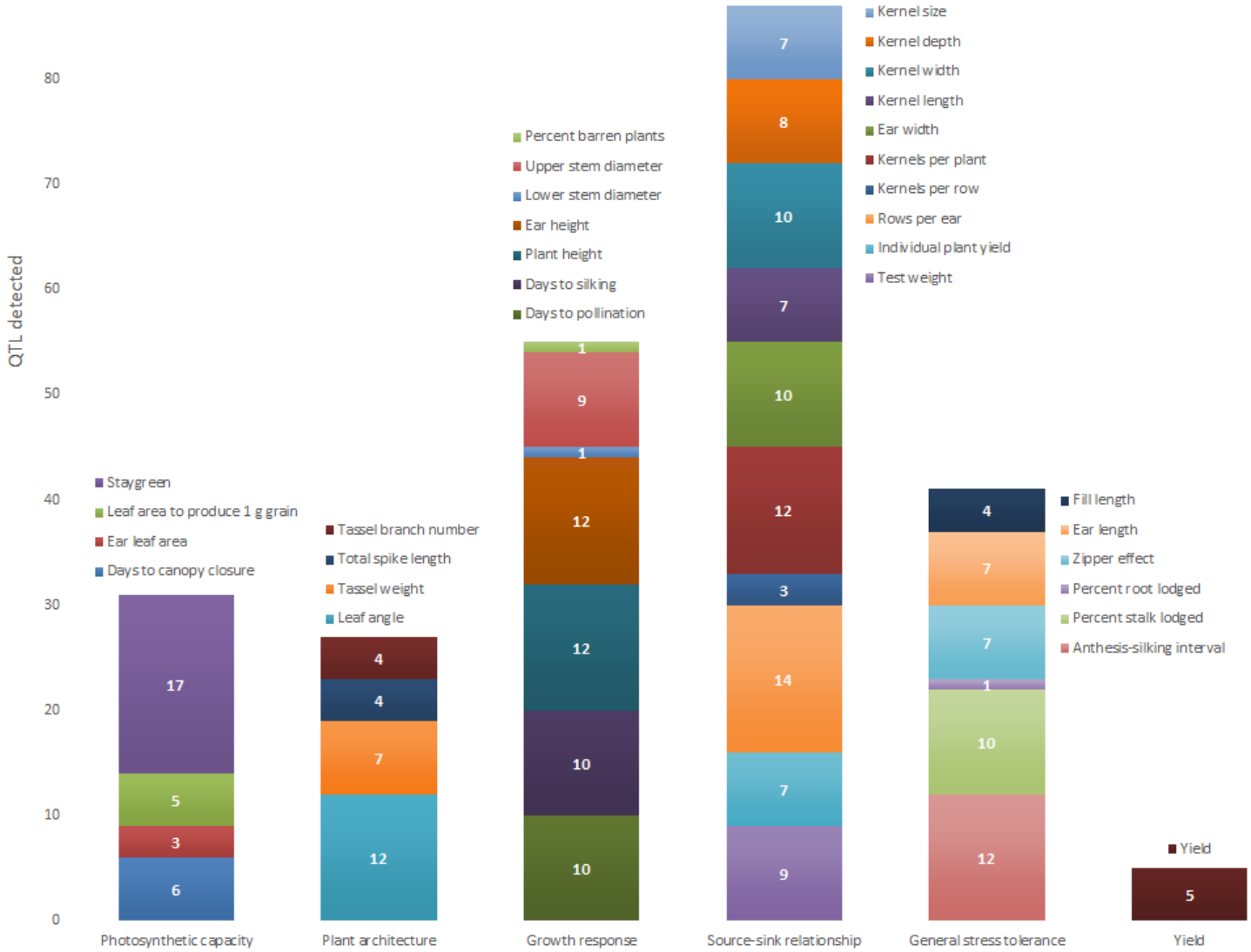


Figure 10. The number of QTL identified for each trait. Each trait is shown in a column representing the corresponding category, and traits are listed above (or to the side of) the columns in the order that each bar segment is presented (i.e. staygreen is listed first, corresponding to the top bar segment having 17 QTL identified).

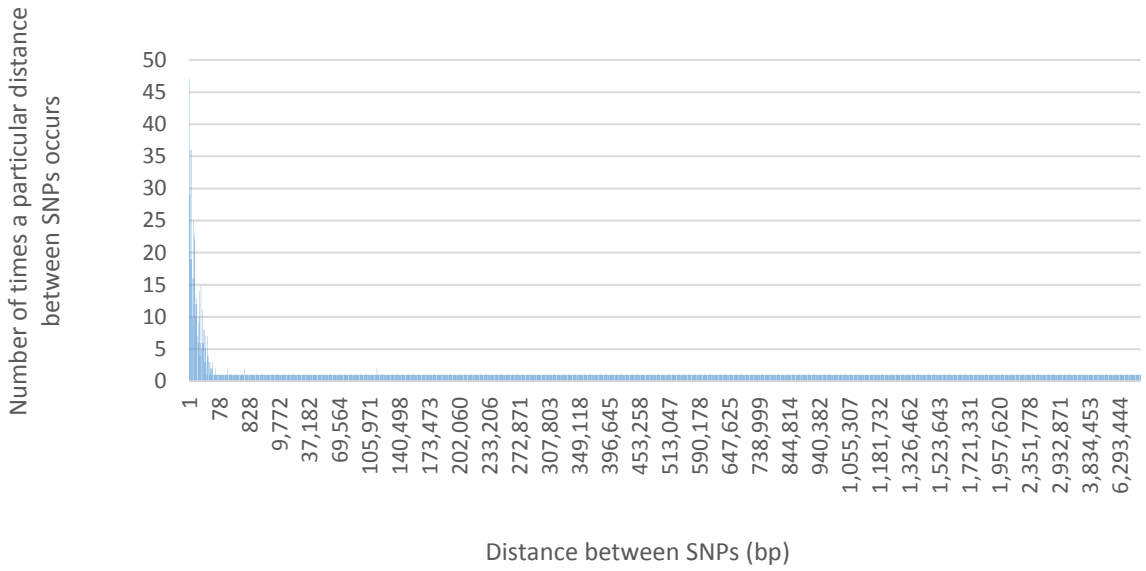


Figure 11. This is the distribution of distances between the SNPs used in the GWAS analysis. Very close inter-marker spacing was repeated with high frequency (left side of graph) compared to larger distances, as expected. Starting with 53 base pair spacing, within the next 1,793 spacing intervals, only four were repeated twice.

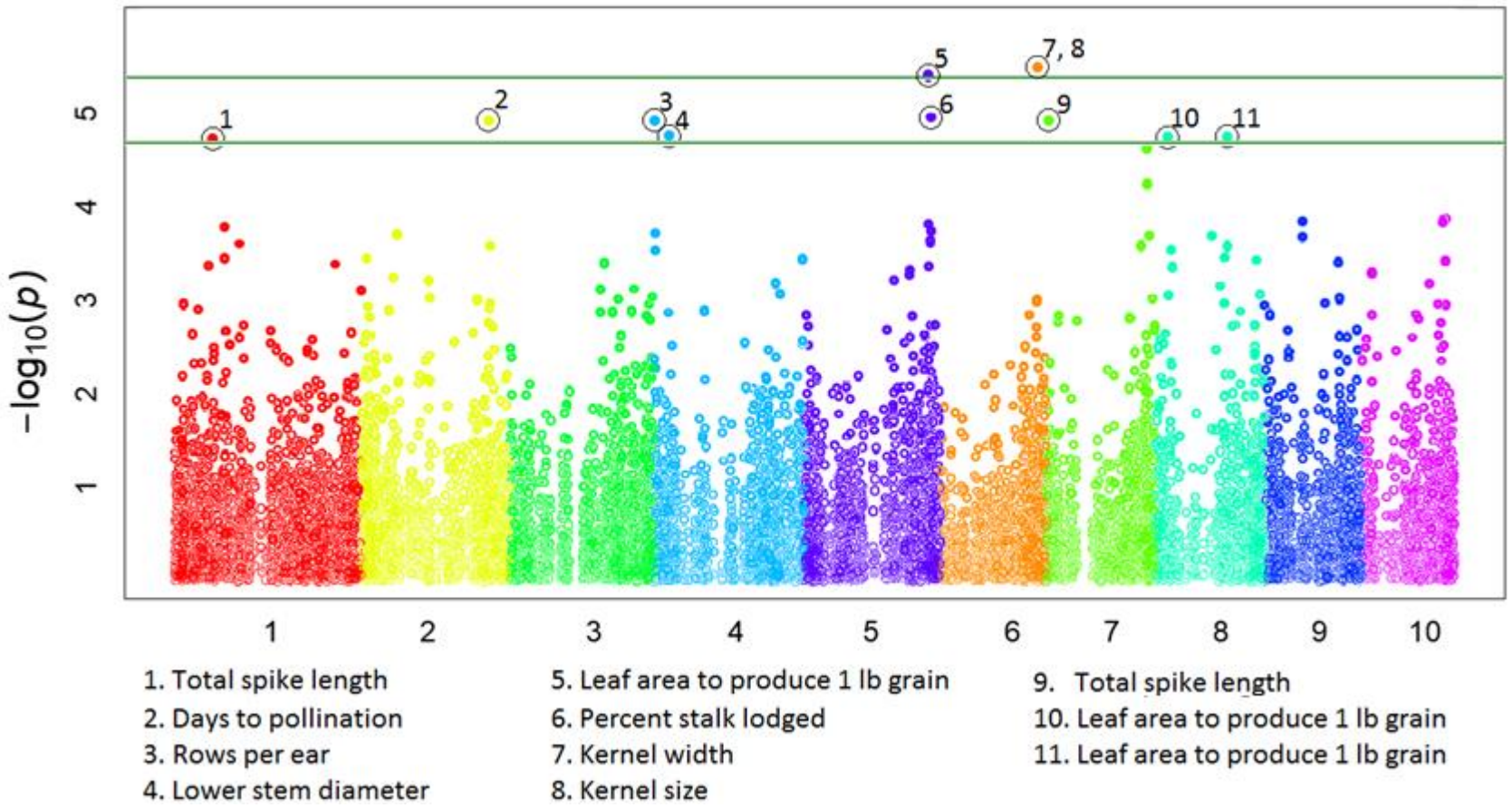


Figure 12. The genome-wide Manhattan plot showing 11 SNP-traits associations detected using GWAS analysis. The lower green line signifies the 0.05 FDR adjusted *P*-value threshold and the upper green line signifies a threshold of 0.01.

Appendix

Table A 1. Location, planting data, harvest date and precipitation data (inches) for each environment. Month totals and grand totals are listed at the bottom.

		Env1	Env2	Env3	Env4	Env5
	Location	Urbana	Savoy	Urbana	Savoy	Monmouth
	Plant date	4/25/2012	5/10/2012	5/14/2013	5/15/2013	5/17/2013
	Harvest date	10/19/2012	11/1/2012	10/23/2013	10/11/2013	10/17/2013
Week ending	Week number	Precipitation	Precipitation	Precipitation	Precipitation	Precipitation
5/4	1	1.51	-	-	-	-
5/11	2	0.59	-	-	-	-
5/18	3	0.00	0.00	-	-	-
5/25	4	0.92	0.92	1.14	1.14	1.14
6/1	5	1.55	1.55	2.56	2.56	5.69
6/8	6	0.31	0.31	0.01	0.01	0.10
6/15	7	0.63	0.63	0.39	0.39	0.00
6/22	8	0.84	0.84	1.51	1.51	0.30
6/29	9	0.00	0.00	2.89	2.89	1.23
7/6	10	0.04	0.04	0.23	0.23	0.10
7/13	11	0.16	0.16	1.24	1.24	0.20
7/20	12	0.41	0.41	0.05	0.05	0.00
7/27	13	0.00	0.00	1.69	1.69	1.02
8/3	14	0.00	0.00	0.61	0.61	0.82
8/10	15	1.31	1.31	0.00	0.00	0.15
8/17	16	2.15	2.15	0.00	0.00	0.00
8/24	17	0.00	0.00	0.01	0.01	0.00
8/31	18	2.14	2.14	0.13	0.13	0.00
9/7	19	4.23	4.23	0.00	0.00	0.00
9/14	20	0.28	0.28	0.04	0.04	0.06
9/21	21	0.77	0.77	0.35	0.35	1.11

Table A 1. (cont.)

		Env1	Env2	Env3	Env4	Env5
9/28	22	0.33	0.33	0.00	0.00	0.00
10/5	23	1.28	1.28	1.33	1.33	0.37
10/12	24	0.03	0.03	0.13	0.13	0.08
10/19	25	2.04	2.04	0.39	-	0.23
10/26	26	-	2.07	-	-	-
May total	-	3.02	0.92	1.14	1.14	1.14
June total	-	3.33	3.33	7.36	7.36	7.32
July total	-	0.61	0.61	3.21	3.21	1.32
August total	-	5.60	5.60	0.75	0.75	0.97
September total	-	5.61	5.61	0.39	0.39	1.17
October total	-	3.35	5.42	1.85	1.46	0.68
Totals	-	21.52	21.49	14.7	14.31	12.6

Table A 2. Location, planting data, harvest date and maximum and minimum air temperature (°C) for each environment. Monthly average maximum and minimum air temperature are listed at the bottom.

		Env1		Env2		Env3		Env4		Env5	
	Location	Urbana		Savoy		Urbana		Savoy		Monmouth	
	Plant date	4/25/2012		5/10/2012		5/14/2013		5/15/2013		5/17/2013	
	Harvest date	10/19/2012		10/16/2012		10/23/2013		10/11/2013		10/17/2013	
Week ending	Week number	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min
5/4	1	23.0	12.8	-		-		-		-	
5/11	2	25.2	12.0	-		-		-		-	
5/18	3	26.5	10.7	26.5	10.7	-		-		-	
5/25	4	28.5	14.1	28.5	14.1	23.8	11.7	23.8	11.7	22.2	12.4
6/1	5	27.3	15.9	27.3	15.9	25.7	15.6	25.7	15.6	23.7	15.3
6/8	6	25.7	12.4	25.7	12.4	24.2	16.5	24.2	16.5	21.6	12.2
6/15	7	29.7	14.7	29.7	14.7	29.0	16.1	29.0	16.1	28.0	17.2
6/22	8	31.4	18.5	31.4	18.5	30.4	17.4	30.4	17.4	30.0	18.3
6/29	9	32.3	16.5	32.3	16.5	29.3	18.8	29.3	18.8	29.0	19.2
7/6	10	36.8	21.5	36.8	21.5	25.6	16.3	25.6	16.3	27.6	15.0
7/13	11	34.2	19.9	34.2	19.9	30.1	18.3	30.1	18.3	29.1	17.5
7/20	12	34.5	21.0	34.5	21.0	33.2	21.0	33.2	21.0	32.5	21.0
7/27	13	35.0	21.1	35.0	21.1	26.2	15.9	26.2	15.9	26.0	14.2
8/3	14	34.4	18.3	34.4	18.3	25.9	15.1	25.9	15.1	25.2	14.1
8/10	15	32.7	18.7	32.7	18.7	27.9	17.7	27.9	17.7	27.5	15.3
8/17	16	26.4	15.6	26.4	15.6	26.3	13.8	26.3	13.8	25.5	10.9
8/24	17	30.2	14.7	30.2	14.7	30.6	17.4	30.6	17.4	28.7	16.0
8/31	18	31.4	17.6	31.4	17.6	33.7	19.0	33.7	19.0	33.2	30.2
9/7	19	28.3	20.0	28.3	20.0	29.6	15.9	29.6	15.9	29.7	13.1
9/14	20	26.0	12.0	26.0	12.0	30.9	16.6	30.9	16.6	29.2	15.1
9/21	21	25.0	9.4	25.0	9.4	26.4	14.2	26.4	14.2	24.1	11.7
9/28	22	20.6	9.1	20.6	9.1	27.5	10.5	27.5	10.5	25.4	10.3

Table A 2. (cont.)

Week ending	Week number	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min
10/5	23	20.1	9.5	20.1	9.5	27.8	15.0	27.8	15.0	26.6	11.9
10/12	24	14.4	0.8	14.4	0.8	24.0	8.8	24.0	8.8	22.0	7.1
10/19	25	18.0	7.1	18.0	7.1	16.6	6.2	-		16.2	4.3
10/26	26	-		19.5	10.0	-		-		-	
May avg.	-	23.9	10.6	23.9	10.6	23.9	10.6	23.9	10.6	23.5	10.3
June avg.	-	28.5	15.8	28.5	15.8	28.5	15.8	28.5	15.8	28.1	15.7
July avg.	-	29.0	17.7	29.0	17.7	29.0	17.7	29.0	17.7	29.9	17.7
August avg.	-	28.3	16.4	28.3	16.4	28.3	16.4	28.3	16.4	29.1	16.6
September avg.	-	25.6	11.7	25.6	11.7	25.6	11.7	25.6	11.7	25.6	11.9
October avg.	-	18.6	5.6	18.6	5.6	18.6	5.6	18.6	5.6	18.8	6.1

Table A 3. The correlation matrix from 2012 phenotypic data, showing r value and significance for all trait-trait combinations. Traits are abbreviated and follow the same order as Table 3.

	Yield	Canopy	ELA	TLA	LAI	LATPg	SG	LAN	TW
Yield	1.00	-0.07	-0.07	-0.07	-0.10	-0.77	0.24	0.08	-0.07
		0.22	0.22	0.22	0.09	<.0001	<.0001	0.19	0.24
Canopy	-0.07	1.00	-0.09	-0.09	-0.09	0.15	-0.19	-0.08	0.04
	0.22		0.12	0.12	0.13	0.01	0.00	0.14	0.48
ELA	-0.07	-0.09	1.00	1.00	0.96	0.32	-0.20	-0.34	0.17
	0.22	0.12		<.0001	<.0001	<.0001	0.00	<.0001	0.00
TLA	-0.07	-0.09	1.00	1.00	0.96	0.32	-0.20	-0.34	0.17
	0.22	0.12	<.0001		<.0001	<.0001	0.00	<.0001	0.00
LAI	-0.10	-0.09	0.96	0.96	1.00	0.35	-0.20	-0.34	0.13
	0.09	0.13	<.0001	<.0001		<.0001	0.00	<.0001	0.02
LATPg	-0.77	0.15	0.32	0.32	0.35	1.00	-0.46	-0.26	0.04
	<.0001	0.01	<.0001	<.0001	<.0001		<.0001	<.0001	0.50
SG	0.24	-0.19	-0.20	-0.20	-0.20	-0.46	1.00	0.39	-0.06
	<.0001	0.00	0.00	0.00	0.00	<.0001		<.0001	0.32
LAN	0.08	-0.08	-0.34	-0.34	-0.34	-0.26	0.39	1.00	-0.09
	0.19	0.14	<.0001	<.0001	<.0001	<.0001	<.0001		0.13
TW	-0.07	0.04	0.17	0.17	0.13	0.04	-0.06	-0.09	1.00
	0.24	0.48	0.00	0.00	0.02	0.50	0.32	0.13	
TSL	-0.06	-0.06	0.32	0.32	0.30	0.02	0.06	0.07	0.42
	0.32	0.29	<.0001	<.0001	<.0001	0.77	0.30	0.25	<.0001
TBN	-0.25	-0.02	0.03	0.03	0.04	0.33	-0.20	-0.25	0.49
	<.0001	0.74	0.54	0.54	0.43	<.0001	0.00	<.0001	<.0001
DTA	-0.43	0.20	0.24	0.24	0.26	0.77	-0.59	-0.44	0.04
	<.0001	0.00	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	0.45
DTS	-0.58	0.09	0.22	0.22	0.24	0.72	-0.54	-0.49	0.16
	<.0001	0.11	0.00	0.00	<.0001	<.0001	<.0001	<.0001	0.00
PH	-0.21	0.05	0.16	0.16	0.15	0.42	-0.40	-0.27	-0.09
	0.00	0.39	0.00	0.00	0.01	<.0001	<.0001	<.0001	0.12
EH	-0.15	0.05	-0.03	-0.03	-0.02	0.32	-0.09	0.00	-0.02
	0.01	0.42	0.63	0.63	0.73	<.0001	0.11	0.95	0.74
LSD	-0.01	-0.02	0.15	0.15	0.12	0.17	-0.26	-0.33	0.24
	0.85	0.77	0.01	0.01	0.03	0.00	<.0001	<.0001	<.0001
USD	-0.10	0.05	0.27	0.27	0.25	0.18	-0.26	-0.10	0.37
	0.07	0.40	<.0001	<.0001	<.0001	0.00	<.0001	0.07	<.0001

Table A 3. (cont.)

	TSL	TBN	DTA	DTS	PH	EH	LSD	USD	PB
Yield	-0.06	-0.25	-0.43	-0.58	-0.21	-0.15	-0.01	-0.10	-0.63
	0.32	<.0001	<.0001	<.0001	0.00	0.01	0.85	0.07	<.0001
Canopy	-0.06	-0.02	0.20	0.09	0.05	0.05	-0.02	0.05	0.08
	0.29	0.74	0.00	0.11	0.39	0.42	0.77	0.40	0.16
ELA	0.32	0.03	0.24	0.22	0.16	-0.03	0.15	0.27	0.20
	<.0001	0.54	<.0001	0.00	0.00	0.63	0.01	<.0001	0.00
TLA	0.32	0.03	0.24	0.22	0.16	-0.03	0.15	0.27	0.20
	<.0001	0.54	<.0001	0.00	0.00	0.63	0.01	<.0001	0.00
LAI	0.30	0.04	0.26	0.24	0.15	-0.02	0.12	0.25	0.18
	<.0001	0.43	<.0001	<.0001	0.01	0.73	0.03	<.0001	0.00
LATPg	0.02	0.33	0.77	0.72	0.42	0.32	0.17	0.18	0.63
	0.77	<.0001	<.0001	<.0001	<.0001	<.0001	0.00	0.00	<.0001
SG	0.06	-0.20	-0.59	-0.54	-0.40	-0.09	-0.26	-0.26	-0.25
	0.30	0.00	<.0001	<.0001	<.0001	0.11	<.0001	<.0001	<.0001
LAN	0.07	-0.25	-0.44	-0.49	-0.27	0.00	-0.33	-0.10	-0.09
	0.25	<.0001	<.0001	<.0001	<.0001	0.95	<.0001	0.07	0.13
TW	0.42	0.49	0.04	0.16	-0.09	-0.02	0.24	0.37	0.03
	<.0001	<.0001	0.45	0.00	0.12	0.74	<.0001	<.0001	0.59
TSL	1.00	-0.08	-0.18	0.03	0.00	-0.14	-0.02	0.40	-0.05
		0.14	0.00	0.58	0.97	0.02	0.77	<.0001	0.37
TBN	-0.08	1.00	0.49	0.55	0.30	0.31	0.43	0.05	0.22
	0.14		<.0001	<.0001	<.0001	<.0001	<.0001	0.38	<.0001
DTA	-0.18	0.49	1.00	0.75	0.52	0.46	0.34	0.10	0.41
	0.00	<.0001		<.0001	<.0001	<.0001	<.0001	0.08	<.0001
DTS	0.03	0.55	0.75	1.00	0.46	0.26	0.31	0.13	0.39
	0.58	<.0001	<.0001		<.0001	<.0001	<.0001	0.02	<.0001
PH	0.00	0.30	0.52	0.46	1.00	0.48	0.26	0.13	0.27
	0.97	<.0001	<.0001	<.0001		<.0001	<.0001	0.02	<.0001
EH	-0.14	0.31	0.46	0.26	0.48	1.00	0.23	0.13	0.25
	0.02	<.0001	<.0001	<.0001	<.0001		<.0001	0.03	<.0001
LSD	-0.02	0.43	0.34	0.31	0.26	0.23	1.00	0.16	0.07
	0.77	<.0001	<.0001	<.0001	<.0001	<.0001		0.00	0.23
USD	0.40	0.05	0.10	0.13	0.13	0.13	0.16	1.00	0.19
	<.0001	0.38	0.08	0.02	0.02	0.03	0.00		0.00

Table A 3. (cont.)

	TWT	IPY	Nrows	Krows	KpP	EW	KL	KW	KD
Yield	0.27	0.99	0.23	0.39	0.41	0.30	0.05	-0.22	-0.39
	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	0.42	0.00	<.0001
Canopy	-0.07	-0.08	0.06	-0.05	-0.01	0.12	0.05	0.05	0.10
	0.27	0.19	0.27	0.42	0.89	0.03	0.42	0.35	0.08
ELA	0.02	-0.06	-0.10	0.17	0.09	0.08	0.12	0.27	0.06
	0.78	0.28	0.07	0.00	0.13	0.15	0.03	<.0001	0.26
TLA	0.02	-0.06	-0.10	0.17	0.09	0.08	0.12	0.27	0.06
	0.78	0.28	0.07	0.00	0.13	0.15	0.03	<.0001	0.26
LAI	0.03	-0.13	-0.09	0.15	0.07	0.06	0.12	0.24	0.05
	0.62	0.03	0.10	0.01	0.19	0.28	0.04	<.0001	0.41
LATPg	-0.08	-0.77	-0.22	-0.27	-0.30	-0.24	0.04	0.27	0.39
	0.18	<.0001	0.00	<.0001	<.0001	<.0001	0.48	<.0001	<.0001
SG	0.11	0.24	0.11	0.29	0.28	-0.05	-0.13	-0.25	-0.50
	0.07	<.0001	0.06	<.0001	<.0001	0.41	0.02	<.0001	<.0001
LAN	-0.19	0.08	-0.13	0.09	-0.01	-0.08	-0.13	0.00	-0.18
	0.00	0.15	0.02	0.12	0.92	0.16	0.02	0.99	0.00
TW	-0.03	-0.05	0.10	0.17	0.18	0.12	-0.05	-0.04	-0.06
	0.63	0.40	0.09	0.00	0.00	0.03	0.42	0.44	0.28
TSL	-0.04	-0.05	-0.20	0.10	-0.03	-0.10	-0.17	0.19	0.04
	0.54	0.43	0.00	0.08	0.61	0.09	0.00	0.00	0.50
TBN	0.11	-0.26	0.16	0.06	0.14	-0.03	0.11	-0.22	0.01
	0.07	<.0001	0.01	0.28	0.01	0.56	0.04	<.0001	0.80
DTA	0.12	-0.45	-0.03	-0.15	-0.11	-0.10	0.11	0.09	0.32
	0.04	<.0001	0.63	0.01	0.05	0.08	0.06	0.10	<.0001
DTS	0.08	-0.60	-0.11	-0.26	-0.25	-0.21	0.02	0.11	0.39
	0.19	<.0001	0.05	<.0001	<.0001	0.00	0.74	0.05	<.0001
PH	0.06	-0.22	-0.12	-0.10	-0.12	-0.12	0.11	0.15	0.28
	0.35	0.00	0.04	0.07	0.04	0.04	0.05	0.01	<.0001
EH	0.06	-0.16	0.02	0.05	0.06	0.06	0.19	0.04	0.02
	0.35	0.00	0.77	0.37	0.27	0.32	0.00	0.52	0.78
LSD	0.09	0.00	0.06	0.14	0.14	0.09	0.14	-0.09	0.02
	0.15	0.98	0.32	0.02	0.01	0.10	0.01	0.13	0.77
USD	-0.08	-0.09	-0.24	0.01	-0.12	0.17	0.24	0.45	0.13
	0.17	0.11	<.0001	0.84	0.04	0.00	<.0001	<.0001	0.02

Table A 3. (cont.)

	KS	ASI	PSL	PRL	Zipper	EL	Fill
Yield	-0.33	-0.57	0.16	0.19	-0.18	0.21	0.23
	<.0001	<.0001	0.01	0.00	0.00	0.00	<.0001
Canopy	0.11	0.07	-0.16	-0.18	-0.09	0.06	0.03
	0.06	0.22	0.00	0.00	0.11	0.33	0.56
ELA	0.23	0.20	-0.28	0.08	0.02	0.35	0.33
	<.0001	0.00	<.0001	0.14	0.66	<.0001	<.0001
TLA	0.23	0.20	-0.28	0.08	0.02	0.35	0.33
	<.0001	0.00	<.0001	0.14	0.66	<.0001	<.0001
LAI	0.20	0.23	-0.25	0.12	0.04	0.30	0.29
	0.00	<.0001	<.0001	0.04	0.45	<.0001	<.0001
LATPg	0.39	0.66	-0.29	-0.24	0.21	-0.07	-0.09
	<.0001	<.0001	<.0001	<.0001	0.00	0.24	0.13
SG	-0.49	-0.50	0.35	0.27	-0.27	-0.03	0.01
	<.0001	<.0001	<.0001	<.0001	<.0001	0.56	0.87
LAN	-0.16	-0.47	0.17	0.16	-0.19	0.07	0.03
	0.00	<.0001	0.00	0.00	0.00	0.24	0.56
TW	-0.08	0.18	0.11	0.13	0.08	0.22	0.19
	0.16	0.00	0.05	0.02	0.18	0.00	0.00
TSL	0.05	0.07	0.07	0.23	-0.05	0.40	0.26
	0.35	0.23	0.20	<.0001	0.39	<.0001	<.0001
TBN	-0.06	0.54	0.14	-0.12	0.16	-0.12	0.02
	0.30	<.0001	0.01	0.04	0.01	0.04	0.77
DTA	0.29	0.67	-0.20	-0.32	0.14	-0.04	0.00
	<.0001	<.0001	0.00	<.0001	0.01	0.50	0.94
DTS	0.30	0.99	-0.15	-0.24	0.25	-0.11	-0.08
	<.0001	<.0001	0.01	<.0001	<.0001	0.06	0.14
PH	0.29	0.43	-0.12	-0.11	0.09	0.04	0.05
	<.0001	<.0001	0.03	0.05	0.11	0.45	0.34
EH	0.11	0.21	0.08	-0.05	0.12	-0.10	-0.05
	0.06	0.00	0.19	0.41	0.04	0.07	0.36
LSD	0.03	0.30	0.02	-0.01	0.19	0.07	0.15
	0.65	<.0001	0.72	0.84	0.00	0.22	0.01
USD	0.41	0.13	-0.18	0.05	0.22	0.14	0.07
	<.0001	0.02	0.00	0.42	<.0001	0.02	0.22

Table A 3. (cont.)

	Yield	Canopy	ELA	TLA	LAI	LATPg	SG	LAN	TW
PB	-0.63	0.08	0.20	0.20	0.18	0.63	-0.25	-0.09	0.03
	<.0001	0.16	0.00	0.00	0.00	<.0001	<.0001	0.13	0.59
TWT	0.27	-0.07	0.02	0.02	0.03	-0.08	0.11	-0.19	-0.03
	<.0001	0.27	0.78	0.78	0.62	0.18	0.07	0.00	0.63
IPY	0.99	-0.08	-0.06	-0.06	-0.13	-0.77	0.24	0.08	-0.05
	<.0001	0.19	0.28	0.28	0.03	<.0001	<.0001	0.15	0.40
Nrows	0.23	0.06	-0.10	-0.10	-0.09	-0.22	0.11	-0.13	0.10
	<.0001	0.27	0.07	0.07	0.10	0.00	0.06	0.02	0.09
Krows	0.39	-0.05	0.17	0.17	0.15	-0.27	0.29	0.09	0.17
	<.0001	0.42	0.00	0.00	0.01	<.0001	<.0001	0.12	0.00
KpP	0.41	-0.01	0.09	0.09	0.07	-0.30	0.28	-0.01	0.18
	<.0001	0.89	0.13	0.13	0.19	<.0001	<.0001	0.92	0.00
EW	0.30	0.12	0.08	0.08	0.06	-0.24	-0.05	-0.08	0.12
	<.0001	0.03	0.15	0.15	0.28	<.0001	0.41	0.16	0.03
KL	0.05	0.05	0.12	0.12	0.12	0.04	-0.13	-0.13	-0.05
	0.42	0.42	0.03	0.03	0.04	0.48	0.02	0.02	0.42
KW	-0.22	0.05	0.27	0.27	0.24	0.27	-0.25	0.00	-0.04
	0.00	0.35	<.0001	<.0001	<.0001	<.0001	<.0001	0.99	0.44
KD	-0.39	0.10	0.06	0.06	0.05	0.39	-0.50	-0.18	-0.06
	<.0001	0.08	0.26	0.26	0.41	<.0001	<.0001	0.00	0.28
KS	-0.33	0.11	0.23	0.23	0.20	0.39	-0.49	-0.16	-0.08
	<.0001	0.06	<.0001	<.0001	0.00	<.0001	<.0001	0.00	0.16
ASI	-0.57	0.07	0.20	0.20	0.23	0.66	-0.50	-0.47	0.18
	<.0001	0.22	0.00	0.00	<.0001	<.0001	<.0001	<.0001	0.00
PSL	0.16	-0.16	-0.28	-0.28	-0.25	-0.29	0.35	0.17	0.11
	0.01	0.00	<.0001	<.0001	<.0001	<.0001	<.0001	0.00	0.05
PRL	0.19	-0.18	0.08	0.08	0.12	-0.24	0.27	0.16	0.13
	0.00	0.00	0.14	0.14	0.04	<.0001	<.0001	0.00	0.02
Zipper	-0.18	-0.09	0.02	0.02	0.04	0.21	-0.27	-0.19	0.08
	0.00	0.11	0.66	0.66	0.45	0.00	<.0001	0.00	0.18
EL	0.21	0.06	0.35	0.35	0.30	-0.07	-0.03	0.07	0.22
	0.00	0.33	<.0001	<.0001	<.0001	0.24	0.56	0.24	0.00
Fill	0.23	0.03	0.33	0.33	0.29	-0.09	0.01	0.03	0.19
	<.0001	0.56	<.0001	<.0001	<.0001	0.13	0.87	0.56	0.00

Table A 3. (cont.)

	TSL	TBN	DTA	DTS	PH	EH	LSD	USD	PB
PB	-0.05	0.22	0.41	0.39	0.27	0.25	0.07	0.19	1.00
	0.37	<.0001	<.0001	<.0001	<.0001	<.0001	0.23	0.00	
TWT	-0.04	0.11	0.12	0.08	0.06	0.06	0.09	-0.08	-0.22
	0.54	0.07	0.04	0.19	0.35	0.35	0.15	0.17	0.00
IPY	-0.05	-0.26	-0.45	-0.60	-0.22	-0.16	0.00	-0.09	-0.61
	0.43	<.0001	<.0001	<.0001	0.00	0.00	0.98	0.11	<.0001
Nrows	-0.20	0.16	-0.03	-0.11	-0.12	0.02	0.06	-0.24	-0.05
	0.00	0.01	0.63	0.05	0.04	0.77	0.32	<.0001	0.39
Krows	0.10	0.06	-0.15	-0.26	-0.10	0.05	0.14	0.01	-0.10
	0.08	0.28	0.01	<.0001	0.07	0.37	0.02	0.84	0.07
KpP	-0.03	0.14	-0.11	-0.25	-0.12	0.06	0.14	-0.12	-0.09
	0.61	0.01	0.05	<.0001	0.04	0.27	0.01	0.04	0.13
EW	-0.10	-0.03	-0.10	-0.21	-0.12	0.06	0.09	0.17	0.06
	0.09	0.56	0.08	0.00	0.04	0.32	0.10	0.00	0.32
KL	-0.17	0.11	0.11	0.02	0.11	0.19	0.14	0.24	0.36
	0.00	0.04	0.06	0.74	0.05	0.00	0.01	<.0001	<.0001
KW	0.19	-0.22	0.09	0.11	0.15	0.04	-0.09	0.45	0.22
	0.00	<.0001	0.10	0.05	0.01	0.52	0.13	<.0001	0.00
KD	0.04	0.01	0.32	0.39	0.28	0.02	0.02	0.13	0.15
	0.50	0.80	<.0001	<.0001	<.0001	0.78	0.77	0.02	0.01
KS	0.05	-0.06	0.29	0.30	0.29	0.11	0.03	0.41	0.35
	0.35	0.30	<.0001	<.0001	<.0001	0.06	0.65	<.0001	<.0001
ASI	0.07	0.54	0.67	0.99	0.43	0.21	0.30	0.13	0.37
	0.23	<.0001	<.0001	<.0001	<.0001	0.00	<.0001	0.02	<.0001
PSL	0.07	0.14	-0.20	-0.15	-0.12	0.08	0.02	-0.18	-0.33
	0.20	0.01	0.00	0.01	0.03	0.19	0.72	0.00	<.0001
PRL	0.23	-0.12	-0.32	-0.24	-0.11	-0.05	-0.01	0.05	-0.28
	<.0001	0.04	<.0001	<.0001	0.05	0.41	0.84	0.42	<.0001
Zipper	-0.05	0.16	0.14	0.25	0.09	0.12	0.19	0.22	0.05
	0.39	0.01	0.01	<.0001	0.11	0.04	0.00	<.0001	0.38
EL	0.40	-0.12	-0.04	-0.11	0.04	-0.10	0.07	0.14	-0.08
	<.0001	0.04	0.50	0.06	0.45	0.07	0.22	0.02	0.18
Fill	0.26	0.02	0.00	-0.08	0.05	-0.05	0.15	0.07	-0.04
	<.0001	0.77	0.94	0.14	0.34	0.36	0.01	0.22	0.50

Table A 3. (cont.)

	TWT	IPY	Nrows	Krows	KpP	EW	KL	KW	KD
PB	-0.22	-0.61	-0.05	-0.10	-0.09	0.06	0.36	0.22	0.15
	0.00	<.0001	0.39	0.07	0.13	0.32	<.0001	0.00	0.01
TWT	1.00	0.25	0.01	0.20	0.16	-0.16	-0.13	-0.20	-0.20
		<.0001	0.85	0.00	0.01	0.01	0.03	0.00	0.00
IPY	0.25	1.00	0.22	0.40	0.41	0.30	0.05	-0.20	-0.38
	<.0001		0.00	<.0001	<.0001	<.0001	0.36	0.00	<.0001
Nrows	0.01	0.22	1.00	0.16	0.66	0.50	0.20	-0.68	-0.21
	0.85	0.00		0.00	<.0001	<.0001	0.00	<.0001	0.00
Krows	0.20	0.40	0.16	1.00	0.84	0.23	0.12	-0.21	-0.68
	0.00	<.0001	0.00		<.0001	<.0001	0.03	0.00	<.0001
KpP	0.16	0.41	0.66	0.84	1.00	0.44	0.20	-0.52	-0.61
	0.01	<.0001	<.0001	<.0001		<.0001	0.00	<.0001	<.0001
EW	-0.16	0.30	0.50	0.23	0.44	1.00	0.61	0.00	-0.26
	0.01	<.0001	<.0001	<.0001	<.0001		<.0001	0.98	<.0001
KL	-0.13	0.05	0.20	0.12	0.20	0.61	1.00	0.17	-0.21
	0.03	0.36	0.00	0.03	0.00	<.0001		0.00	0.00
KW	-0.20	-0.20	-0.68	-0.21	-0.52	0.00	0.17	1.00	0.33
	0.00	0.00	<.0001	0.00	<.0001	0.98	0.00		<.0001
KD	-0.20	-0.38	-0.21	-0.68	-0.61	-0.26	-0.21	0.33	1.00
	0.00	<.0001	0.00	<.0001	<.0001	<.0001	0.00	<.0001	
KS	-0.27	-0.32	-0.39	-0.48	-0.57	0.10	0.38	0.79	0.70
	<.0001	<.0001	<.0001	<.0001	<.0001	0.09	<.0001	<.0001	<.0001
ASI	0.07	-0.59	-0.12	-0.27	-0.26	-0.21	0.00	0.10	0.37
	0.25	<.0001	0.04	<.0001	<.0001	0.00	0.93	0.07	<.0001
PSL	0.01	0.15	0.13	0.20	0.22	-0.09	-0.21	-0.32	-0.29
	0.87	0.01	0.02	0.00	<.0001	0.12	0.00	<.0001	<.0001
PRL	0.00	0.18	-0.06	0.16	0.09	0.00	-0.16	-0.01	-0.24
	0.95	0.00	0.28	0.01	0.13	0.96	0.00	0.81	<.0001
Zipper	-0.01	-0.17	-0.34	-0.07	-0.24	-0.03	0.02	0.21	-0.02
	0.82	0.00	<.0001	0.23	<.0001	0.58	0.72	0.00	0.66
EL	-0.03	0.23	0.00	0.53	0.41	0.05	-0.20	0.06	-0.02
	0.61	<.0001	0.99	<.0001	<.0001	0.34	0.00	0.32	0.69
Fill	0.06	0.24	0.04	0.71	0.56	0.08	-0.10	-0.05	-0.14
	0.32	<.0001	0.43	<.0001	<.0001	0.18	0.07	0.34	0.01

Table A 3. (cont.)

	KS	ASI	PSL	PRL	Zipper	EL	Fill
PB	0.35	0.37	-0.33	-0.28	0.05	-0.08	-0.04
	<.0001	<.0001	<.0001	<.0001	0.38	0.18	0.50
TWT	-0.27	0.07	0.01	0.00	-0.01	-0.03	0.06
	<.0001	0.25	0.87	0.95	0.82	0.61	0.32
IPY	-0.32	-0.59	0.15	0.18	-0.17	0.23	0.24
	<.0001	<.0001	0.01	0.00	0.00	<.0001	<.0001
Nrows	-0.39	-0.12	0.13	-0.06	-0.34	0.00	0.04
	<.0001	0.04	0.02	0.28	<.0001	0.99	0.43
Krows	-0.48	-0.27	0.20	0.16	-0.07	0.53	0.71
	<.0001	<.0001	0.00	0.01	0.23	<.0001	<.0001
KpP	-0.57	-0.26	0.22	0.09	-0.24	0.41	0.56
	<.0001	<.0001	<.0001	0.13	<.0001	<.0001	<.0001
EW	0.10	-0.21	-0.09	0.00	-0.03	0.05	0.08
	0.09	0.00	0.12	0.96	0.58	0.34	0.18
KL	0.38	0.00	-0.21	-0.16	0.02	-0.20	-0.10
	<.0001	0.93	0.00	0.00	0.72	0.00	0.07
KW	0.79	0.10	-0.32	-0.01	0.21	0.06	-0.05
	<.0001	0.07	<.0001	0.81	0.00	0.32	0.34
KD	0.70	0.37	-0.29	-0.24	-0.02	-0.02	-0.14
	<.0001	<.0001	<.0001	<.0001	0.66	0.69	0.01
KS	1.00	0.28	-0.42	-0.22	0.09	-0.07	-0.16
		<.0001	<.0001	<.0001	0.12	0.22	0.01
ASI	0.28	1.00	-0.13	-0.22	0.26	-0.12	-0.09
	<.0001		0.02	0.00	<.0001	0.04	0.10
PSL	-0.42	-0.13	1.00	0.15	-0.07	0.01	0.06
	<.0001	0.02		0.01	0.21	0.85	0.33
PRL	-0.22	-0.22	0.15	1.00	-0.02	0.12	0.09
	<.0001	0.00	0.01		0.75	0.03	0.11
Zipper	0.09	0.26	-0.07	-0.02	1.00	-0.23	-0.25
	0.12	<.0001	0.21	0.75		<.0001	<.0001
EL	-0.07	-0.12	0.01	0.12	-0.23	1.00	0.88
	0.22	0.04	0.85	0.03	<.0001		<.0001
Fill	-0.16	-0.09	0.06	0.09	-0.25	0.88	1.00
	0.01	0.10	0.33	0.11	<.0001	<.0001	

Table A 4. The correlation matrix from 2013 phenotypic data, showing r value and significance for all trait-trait combinations. Traits are abbreviated and follow the same order as Table 3.

	Yield	Canopy	ELA	TLA	LAI	LATPg	SG	LAN	TW
Yield	1.00	-0.32	0.13	0.13	0.17	-0.80	-0.22	-0.30	-0.11
		<.0001	0.04	0.04	0.01	<.0001	0.00	<.0001	0.09
Canopy	-0.32	1.00	-0.34	-0.34	-0.42	0.06	-0.01	0.30	0.16
	<.0001		<.0001	<.0001	<.0001	0.35	0.88	<.0001	0.01
ELA	0.13	-0.34	1.00	1.00	0.91	0.39	-0.18	-0.39	0.01
	0.04	<.0001		<.0001	<.0001	<.0001	0.00	<.0001	0.84
TLA	0.13	-0.34	1.00	1.00	0.91	0.39	-0.18	-0.39	0.01
	0.04	<.0001	<.0001		<.0001	<.0001	0.00	<.0001	0.86
LAI	0.17	-0.42	0.91	0.91	1.00	0.34	-0.14	-0.38	-0.02
	0.01	<.0001	<.0001	<.0001		<.0001	0.03	<.0001	0.74
LATPg	-0.80	0.06	0.39	0.39	0.34	1.00	0.09	0.02	0.07
	<.0001	0.35	<.0001	<.0001	<.0001		0.16	0.70	0.29
SG	-0.22	-0.01	-0.18	-0.18	-0.14	0.09	1.00	0.21	-0.09
	0.00	0.88	0.00	0.00	0.03	0.16		0.00	0.16
LAN	-0.30	0.30	-0.39	-0.39	-0.38	0.02	0.21	1.00	0.12
	<.0001	<.0001	<.0001	<.0001	<.0001	0.70	0.00		0.06
TW	-0.11	0.16	0.01	0.01	-0.02	0.07	-0.09	0.12	1.00
	0.09	0.01	0.84	0.86	0.74	0.29	0.16	0.06	
TSL	-0.25	0.11	0.16	0.16	0.06	0.26	-0.02	0.09	0.51
	<.0001	0.08	0.02	0.01	0.33	<.0001	0.72	0.17	<.0001
TBN	0.27	-0.37	0.14	0.14	0.16	-0.11	0.23	-0.26	0.18
	<.0001	<.0001	0.03	0.02	0.01	0.08	0.00	<.0001	0.00
DTA	0.41	-0.56	0.42	0.42	0.41	-0.08	-0.17	-0.45	-0.14
	<.0001	<.0001	<.0001	<.0001	<.0001	0.21	0.01	<.0001	0.03
DTS	0.00	-0.24	0.19	0.19	0.20	0.15	-0.05	-0.36	0.15
	0.96	0.00	0.00	0.00	0.00	0.02	0.40	<.0001	0.02
PH	0.43	-0.44	0.24	0.24	0.19	-0.19	-0.04	-0.26	-0.08
	<.0001	<.0001	0.00	0.00	0.00	0.00	0.56	<.0001	0.21
EH	0.46	-0.43	0.15	0.16	0.13	-0.26	0.05	-0.11	-0.05
	<.0001	<.0001	0.02	0.01	0.04	<.0001	0.48	0.08	0.41
USD	-0.08	0.07	0.15	0.16	0.06	0.13	-0.11	0.12	0.17
	0.21	0.29	0.02	0.01	0.32	0.04	0.07	0.06	0.01

Table A 4. (cont.)

	TSL	TBN	DTA	DTS	PH	EH	USD	PB	TWT
Yield	-0.25	0.27	0.41	0.00	0.43	0.46	-0.08	-0.30	0.06
	<.0001	<.0001	<.0001	0.96	<.0001	<.0001	0.21	<.0001	0.32
Canopy	0.11	-0.37	-0.56	-0.24	-0.44	-0.43	0.07	-0.06	-0.08
	0.08	<.0001	<.0001	0.00	<.0001	<.0001	0.29	0.39	0.23
ELA	0.16	0.14	0.42	0.19	0.24	0.15	0.15	0.19	-0.09
	0.02	0.03	<.0001	0.00	0.00	0.02	0.02	0.00	0.17
TLA	0.16	0.14	0.42	0.19	0.24	0.16	0.16	0.19	-0.09
	0.01	0.02	<.0001	0.00	0.00	0.01	0.01	0.00	0.16
LAI	0.06	0.16	0.41	0.20	0.19	0.13	0.06	0.18	-0.07
	0.33	0.01	<.0001	0.00	0.00	0.04	0.32	0.00	0.28
LATPg	0.26	-0.11	-0.08	0.15	-0.19	-0.26	0.13	0.39	-0.08
	<.0001	0.08	0.21	0.02	0.00	<.0001	0.04	<.0001	0.21
SG	-0.02	0.23	-0.17	-0.05	-0.04	0.05	-0.11	-0.14	0.03
	0.72	0.00	0.01	0.40	0.56	0.48	0.07	0.03	0.64
LAN	0.09	-0.26	-0.45	-0.36	-0.26	-0.11	0.12	-0.04	-0.11
	0.17	<.0001	<.0001	<.0001	<.0001	0.08	0.06	0.54	0.07
TW	0.51	0.18	-0.14	0.15	-0.08	-0.05	0.17	0.02	-0.25
	<.0001	0.00	0.03	0.02	0.21	0.41	0.01	0.78	<.0001
TSL	1.00	-0.16	-0.15	0.17	0.00	-0.06	0.26	0.16	-0.06
		0.01	0.02	0.01	0.95	0.38	<.0001	0.01	0.36
TBN	-0.16	1.00	0.37	0.38	0.48	0.37	-0.08	-0.16	-0.15
	0.01		<.0001	<.0001	<.0001	<.0001	0.20	0.01	0.02
DTA	-0.15	0.37	1.00	0.29	0.56	0.55	-0.01	0.08	0.05
	0.02	<.0001		<.0001	<.0001	<.0001	0.86	0.23	0.39
DTS	0.17	0.38	0.29	1.00	0.31	0.06	-0.01	0.09	-0.08
	0.01	<.0001	<.0001		<.0001	0.33	0.82	0.15	0.20
PH	0.00	0.48	0.56	0.31	1.00	0.73	0.00	-0.09	0.03
	0.95	<.0001	<.0001	<.0001		<.0001	0.96	0.17	0.66
EH	-0.06	0.37	0.55	0.06	0.73	1.00	0.05	-0.16	0.06
	0.38	<.0001	<.0001	0.33	<.0001		0.44	0.01	0.37
USD	0.26	-0.08	-0.01	-0.01	0.00	0.05	1.00	0.22	-0.13
	<.0001	0.20	0.86	0.82	0.96	0.44		0.00	0.04

Table A 4. (cont.)

	IPY	Nrows	Krows	KpP	EW	KL	KW	KD	KS
Yield	0.96	0.27	0.14	0.32	0.29	0.33	-0.25	-0.13	-0.10
	<.0001	<.0001	0.03	<.0001	<.0001	<.0001	<.0001	0.04	0.14
Canopy	-0.24	-0.10	-0.22	-0.23	-0.02	-0.10	0.17	0.07	0.11
	0.00	0.14	0.00	0.00	0.75	0.12	0.01	0.25	0.09
ELA	0.19	-0.02	0.23	0.15	0.19	0.21	0.14	0.09	0.22
	0.00	0.71	0.00	0.02	0.00	0.00	0.03	0.15	0.00
TLA	0.19	-0.02	0.23	0.15	0.19	0.21	0.14	0.09	0.22
	0.00	0.73	0.00	0.02	0.00	0.00	0.03	0.16	0.00
LAI	0.13	0.00	0.12	0.09	0.11	0.13	0.07	0.06	0.13
	0.04	0.96	0.06	0.15	0.08	0.04	0.28	0.39	0.05
LATPg	-0.75	-0.23	0.02	-0.17	-0.17	-0.18	0.26	0.15	0.17
	<.0001	0.00	0.70	0.01	0.01	0.01	<.0001	0.02	0.01
SG	-0.21	0.16	0.10	0.19	-0.26	-0.26	-0.28	-0.31	-0.45
	0.00	0.01	0.11	0.00	<.0001	<.0001	<.0001	<.0001	<.0001
LAN	-0.29	-0.25	-0.10	-0.28	-0.13	-0.20	0.27	0.05	0.12
	<.0001	<.0001	0.10	<.0001	0.04	0.00	<.0001	0.46	0.06
TW	-0.13	0.14	-0.07	0.05	0.13	0.02	0.02	0.06	0.06
	0.05	0.03	0.27	0.40	0.05	0.71	0.72	0.32	0.35
TSL	-0.26	-0.24	0.04	-0.16	-0.10	-0.16	0.25	0.22	0.21
	<.0001	0.00	0.51	0.01	0.11	0.01	<.0001	0.00	0.00
TBN	0.27	0.47	0.13	0.46	0.20	0.24	-0.44	-0.24	-0.32
	<.0001	<.0001	0.05	<.0001	0.00	0.00	<.0001	0.00	<.0001
DTA	0.42	0.11	0.22	0.25	0.16	0.22	-0.02	0.01	0.08
	<.0001	0.09	0.00	<.0001	0.01	0.00	0.77	0.89	0.22
DTS	0.00	0.11	-0.04	0.06	-0.09	-0.02	-0.18	0.01	-0.12
	1.00	0.10	0.57	0.39	0.14	0.74	0.01	0.89	0.06
PH	0.45	0.12	0.29	0.31	0.08	0.17	-0.12	0.04	0.01
	<.0001	0.05	<.0001	<.0001	0.20	0.01	0.06	0.52	0.84
EH	0.47	0.10	0.30	0.30	0.13	0.20	-0.06	-0.14	-0.04
	<.0001	0.13	<.0001	<.0001	0.04	0.00	0.32	0.03	0.57
USD	-0.06	-0.20	-0.05	-0.20	0.05	0.09	0.30	0.16	0.31
	0.33	0.00	0.46	0.00	0.46	0.18	<.0001	0.01	<.0001

Table A 4. (cont.)

	ASI	PSL	PRL	Zipper	EL	Fill
Yield	-0.02	-0.21	-0.14	0.00	-0.01	0.09
	0.78	0.00	0.03	0.96	0.83	0.18
Canopy	-0.19	0.13	0.14	-0.17	-0.05	-0.24
	0.00	0.04	0.02	0.01	0.44	0.00
ELA	0.17	-0.08	-0.04	0.07	0.32	0.36
	0.01	0.19	0.56	0.25	<.0001	<.0001
TLA	0.16	-0.08	-0.04	0.06	0.32	0.37
	0.01	0.20	0.56	0.31	<.0001	<.0001
LAI	0.17	-0.09	-0.12	0.13	0.18	0.23
	0.01	0.18	0.06	0.04	0.00	0.00
LATPg	0.14	0.19	0.07	0.03	0.16	0.14
	0.03	0.00	0.27	0.68	0.01	0.03
SG	-0.04	0.31	-0.12	-0.03	-0.26	-0.18
	0.52	<.0001	0.06	0.69	<.0001	0.01
LAN	-0.33	0.14	0.10	-0.10	0.03	-0.16
	<.0001	0.03	0.12	0.11	0.61	0.02
TW	0.18	0.04	-0.06	-0.03	0.15	-0.01
	0.01	0.56	0.32	0.68	0.02	0.83
TSL	0.20	-0.02	-0.01	-0.03	0.35	0.20
	0.00	0.76	0.88	0.68	<.0001	0.00
TBN	0.35	0.09	-0.22	0.09	-0.18	0.01
	<.0001	0.17	0.00	0.15	0.00	0.89
DTA	0.21	-0.08	-0.16	0.06	0.11	0.29
	0.00	0.21	0.01	0.33	0.08	<.0001
DTS	0.99	0.02	-0.08	0.20	-0.10	0.06
	<.0001	0.70	0.19	0.00	0.13	0.37
PH	0.26	-0.01	-0.13	-0.10	0.21	0.37
	<.0001	0.94	0.04	0.10	0.00	<.0001
EH	0.02	0.06	-0.11	-0.09	0.13	0.24
	0.77	0.34	0.09	0.19	0.05	0.00
USD	-0.01	0.04	0.19	-0.08	0.24	0.13
	0.88	0.57	0.00	0.22	0.00	0.04

Table A 4. (cont.)

	Yield	Canopy	ELA	TLA	LAI	LATPg	SG	LAN	TW
PB	-0.30	-0.06	0.19	0.19	0.18	0.39	-0.14	-0.04	0.02
	<.0001	0.39	0.00	0.00	0.00	<.0001	0.03	0.54	0.78
TWT	0.06	-0.08	-0.09	-0.09	-0.07	-0.08	0.03	-0.11	-0.25
	0.32	0.23	0.17	0.16	0.28	0.21	0.64	0.07	<.0001
IPY	0.96	-0.24	0.19	0.19	0.13	-0.75	-0.21	-0.29	-0.13
	<.0001	0.00	0.00	0.00	0.04	<.0001	0.00	<.0001	0.05
Nrows	0.27	-0.10	-0.02	-0.02	0.00	-0.23	0.16	-0.25	0.14
	<.0001	0.14	0.71	0.73	0.96	0.00	0.01	<.0001	0.03
Krows	0.14	-0.22	0.23	0.23	0.12	0.02	0.10	-0.10	-0.07
	0.03	0.00	0.00	0.00	0.06	0.70	0.11	0.10	0.27
KpP	0.32	-0.23	0.15	0.15	0.09	-0.17	0.19	-0.28	0.05
	<.0001	0.00	0.02	0.02	0.15	0.01	0.00	<.0001	0.40
EW	0.29	-0.02	0.19	0.19	0.11	-0.17	-0.26	-0.13	0.13
	<.0001	0.75	0.00	0.00	0.08	0.01	<.0001	0.04	0.05
KL	0.33	-0.10	0.21	0.21	0.13	-0.18	-0.26	-0.20	0.02
	<.0001	0.12	0.00	0.00	0.04	0.01	<.0001	0.00	0.71
KW	-0.25	0.17	0.14	0.14	0.07	0.26	-0.28	0.27	0.02
	<.0001	0.01	0.03	0.03	0.28	<.0001	<.0001	<.0001	0.72
KD	-0.13	0.07	0.09	0.09	0.06	0.15	-0.31	0.05	0.06
	0.04	0.25	0.15	0.16	0.39	0.02	<.0001	0.46	0.32
KS	-0.10	0.11	0.22	0.22	0.13	0.17	-0.45	0.12	0.06
	0.14	0.09	0.00	0.00	0.05	0.01	<.0001	0.06	0.35
ASI	-0.02	-0.19	0.17	0.16	0.17	0.14	-0.04	-0.33	0.18
	0.78	0.00	0.01	0.01	0.01	0.03	0.52	<.0001	0.01
PSL	-0.21	0.13	-0.08	-0.08	-0.09	0.19	0.31	0.14	0.04
	0.00	0.04	0.19	0.20	0.18	0.00	<.0001	0.03	0.56
PRL	-0.14	0.14	-0.04	-0.04	-0.12	0.07	-0.12	0.10	-0.06
	0.03	0.02	0.56	0.56	0.06	0.27	0.06	0.12	0.32
Zipper	0.00	-0.17	0.07	0.06	0.13	0.03	-0.03	-0.10	-0.03
	0.96	0.01	0.25	0.31	0.04	0.68	0.69	0.11	0.68
EL	-0.01	-0.05	0.32	0.32	0.18	0.16	-0.26	0.03	0.15
	0.83	0.44	<.0001	<.0001	0.00	0.01	<.0001	0.61	0.02
Fill	0.09	-0.24	0.36	0.37	0.23	0.14	-0.18	-0.16	-0.01
	0.18	0.00	<.0001	<.0001	0.00	0.03	0.01	0.02	0.83

Table A 4. (cont.)

	TSL	TBN	DTA	DTS	PH	EH	USD	PB	TWT
PB	0.16	-0.16	0.08	0.09	-0.09	-0.16	0.22	1.00	-0.07
	0.01	0.01	0.23	0.15	0.17	0.01	0.00		0.31
TWT	-0.06	-0.15	0.05	-0.08	0.03	0.06	-0.13	-0.07	1.00
	0.36	0.02	0.39	0.20	0.66	0.37	0.04	0.31	
IPY	-0.26	0.27	0.42	0.00	0.45	0.47	-0.06	-0.29	0.06
	<.0001	<.0001	<.0001	1.00	<.0001	<.0001	0.33	<.0001	0.38
Nrows	-0.24	0.47	0.11	0.11	0.12	0.10	-0.20	-0.23	-0.27
	0.00	<.0001	0.09	0.10	0.05	0.13	0.00	0.00	<.0001
Krows	0.04	0.13	0.22	-0.04	0.29	0.30	-0.05	0.02	0.28
	0.51	0.05	0.00	0.57	<.0001	<.0001	0.46	0.74	<.0001
KpP	-0.16	0.46	0.25	0.06	0.31	0.30	-0.20	-0.16	0.00
	0.01	<.0001	<.0001	0.39	<.0001	<.0001	0.00	0.01	0.99
EW	-0.10	0.20	0.16	-0.09	0.08	0.13	0.05	-0.03	-0.35
	0.11	0.00	0.01	0.14	0.20	0.04	0.46	0.64	<.0001
KL	-0.16	0.24	0.22	-0.02	0.17	0.20	0.09	-0.05	-0.31
	0.01	0.00	0.00	0.74	0.01	0.00	0.18	0.46	<.0001
KW	0.25	-0.44	-0.02	-0.18	-0.12	-0.06	0.30	0.27	-0.02
	<.0001	<.0001	0.77	0.01	0.06	0.32	<.0001	<.0001	0.81
KD	0.22	-0.24	0.01	0.01	0.04	-0.14	0.16	0.20	-0.20
	0.00	0.00	0.89	0.89	0.52	0.03	0.01	0.00	0.00
KS	0.21	-0.32	0.08	-0.12	0.01	-0.04	0.31	0.26	-0.25
	0.00	<.0001	0.22	0.06	0.84	0.57	<.0001	<.0001	0.00
ASI	0.20	0.35	0.21	0.99	0.26	0.02	-0.01	0.08	-0.09
	0.00	<.0001	0.00	<.0001	<.0001	0.77	0.88	0.24	0.15
PSL	-0.02	0.09	-0.08	0.02	-0.01	0.06	0.04	-0.12	-0.01
	0.76	0.17	0.21	0.70	0.94	0.34	0.57	0.06	0.90
PRL	-0.01	-0.22	-0.16	-0.08	-0.13	-0.11	0.19	-0.03	-0.12
	0.88	0.00	0.01	0.19	0.04	0.09	0.00	0.67	0.06
Zipper	-0.03	0.09	0.06	0.20	-0.10	-0.09	-0.08	-0.03	-0.02
	0.68	0.15	0.33	0.00	0.10	0.19	0.22	0.61	0.78
EL	0.35	-0.18	0.11	-0.10	0.21	0.13	0.24	0.25	0.03
	<.0001	0.00	0.08	0.13	0.00	0.05	0.00	<.0001	0.64
Fill	0.20	0.01	0.29	0.06	0.37	0.24	0.13	0.23	0.12
	0.00	0.89	<.0001	0.37	<.0001	0.00	0.04	0.00	0.07

Table A 4. (cont.)

	IPY	Nrows	Krows	KpP	EW	KL	KW	KD	KS
PB	-0.29	-0.23	0.02	-0.16	-0.03	-0.05	0.27	0.20	0.26
	<.0001	0.00	0.74	0.01	0.64	0.46	<.0001	0.00	<.0001
TWT	0.06	-0.27	0.28	0.00	-0.35	-0.31	-0.02	-0.20	-0.25
	0.38	<.0001	<.0001	0.99	<.0001	<.0001	0.81	0.00	0.00
IPY	1.00	0.26	0.19	0.35	0.34	0.40	-0.19	-0.12	-0.02
		<.0001	0.00	<.0001	<.0001	<.0001	0.00	0.06	0.73
Nrows	0.26	1.00	-0.14	0.68	0.53	0.33	-0.80	-0.23	-0.51
	<.0001		0.03	<.0001	<.0001	<.0001	<.0001	0.00	<.0001
Krows	0.19	-0.14	1.00	0.63	-0.19	-0.02	0.02	-0.31	-0.16
	0.00	0.03		<.0001	0.00	0.80	0.81	<.0001	0.01
KpP	0.35	0.68	0.63	1.00	0.28	0.25	-0.62	-0.41	-0.52
	<.0001	<.0001	<.0001		<.0001	<.0001	<.0001	<.0001	<.0001
EW	0.34	0.53	-0.19	0.28	1.00	0.68	-0.18	-0.07	0.12
	<.0001	<.0001	0.00	<.0001		<.0001	0.01	0.28	0.06
KL	0.40	0.33	-0.02	0.25	0.68	1.00	-0.08	-0.17	0.26
	<.0001	<.0001	0.80	<.0001	<.0001		0.23	0.01	<.0001
KW	-0.19	-0.80	0.02	-0.62	-0.18	-0.08	1.00	0.36	0.81
	0.00	<.0001	0.81	<.0001	0.01	0.23		<.0001	<.0001
KD	-0.12	-0.23	-0.31	-0.41	-0.07	-0.17	0.36	1.00	0.70
	0.06	0.00	<.0001	<.0001	0.28	0.01	<.0001		<.0001
KS	-0.02	-0.51	-0.16	-0.52	0.12	0.26	0.81	0.70	1.00
	0.73	<.0001	0.01	<.0001	0.06	<.0001	<.0001	<.0001	
ASI	-0.03	0.09	-0.05	0.04	-0.11	-0.04	-0.18	0.00	-0.14
	0.67	0.14	0.45	0.57	0.08	0.50	0.00	0.96	0.03
PSL	-0.20	0.10	0.09	0.13	-0.01	0.04	-0.13	-0.23	-0.18
	0.00	0.13	0.15	0.04	0.89	0.58	0.05	0.00	0.00
PRL	-0.06	-0.13	-0.01	-0.11	0.11	0.08	0.19	0.08	0.20
	0.36	0.05	0.84	0.10	0.08	0.23	0.00	0.21	0.00
Zipper	-0.02	0.06	-0.16	-0.07	0.14	0.08	-0.12	-0.10	-0.10
	0.78	0.32	0.01	0.28	0.03	0.22	0.05	0.12	0.11
EL	0.00	-0.34	0.49	0.10	-0.17	-0.15	0.40	0.38	0.40
	0.95	<.0001	<.0001	0.12	0.01	0.02	<.0001	<.0001	<.0001
Fill	0.11	-0.30	0.73	0.31	-0.26	-0.09	0.28	0.24	0.27
	0.10	<.0001	<.0001	<.0001	<.0001	0.14	<.0001	0.00	<.0001

Table A 4. (cont.)

	ASI	PSL	PRL	Zipper	EL	Fill
PB	0.08	-0.12	-0.03	-0.03	0.25	0.23
	0.24	0.06	0.67	0.61	<.0001	0.00
TWT	-0.09	-0.01	-0.12	-0.02	0.03	0.12
	0.15	0.90	0.06	0.78	0.64	0.07
IPY	-0.03	-0.20	-0.06	-0.02	0.00	0.11
	0.67	0.00	0.36	0.78	0.95	0.10
Nrows	0.09	0.10	-0.13	0.06	-0.34	-0.30
	0.14	0.13	0.05	0.32	<.0001	<.0001
Krows	-0.05	0.09	-0.01	-0.16	0.49	0.73
	0.45	0.15	0.84	0.01	<.0001	<.0001
KpP	0.04	0.13	-0.11	-0.07	0.10	0.31
	0.57	0.04	0.10	0.28	0.12	<.0001
EW	-0.11	-0.01	0.11	0.14	-0.17	-0.26
	0.08	0.89	0.08	0.03	0.01	<.0001
KL	-0.04	0.04	0.08	0.08	-0.15	-0.09
	0.50	0.58	0.23	0.22	0.02	0.14
KW	-0.18	-0.13	0.19	-0.12	0.40	0.28
	0.00	0.05	0.00	0.05	<.0001	<.0001
KD	0.00	-0.23	0.08	-0.10	0.38	0.24
	0.96	0.00	0.21	0.12	<.0001	0.00
KS	-0.14	-0.18	0.20	-0.10	0.40	0.27
	0.03	0.00	0.00	0.11	<.0001	<.0001
ASI	1.00	0.03	-0.08	0.20	-0.11	0.03
		0.69	0.22	0.00	0.09	0.61
PSL	0.03	1.00	-0.05	0.08	-0.11	-0.08
	0.69		0.46	0.20	0.08	0.24
PRL	-0.08	-0.05	1.00	-0.15	0.06	0.04
	0.22	0.46		0.02	0.38	0.50
Zipper	0.20	0.08	-0.15	1.00	-0.33	-0.27
	0.00	0.20	0.02		<.0001	<.0001
EL	-0.11	-0.11	0.06	-0.33	1.00	0.83
	0.09	0.08	0.38	<.0001		<.0001
Fill	0.03	-0.08	0.04	-0.27	0.83	1.00
	0.61	0.24	0.50	<.0001	<.0001	

Table A 5. The 246 QTL detected by QTL mapping within each of the nine subpopulations. QTL are listed for each trait along with chromosome and positional information, as well as which subpopulation and which environment the QTL were detected in. The percent variance explained (σ^2 exp.) is listed along with the LOD score. The QTL are organized by LOD score, with the highest ranking QTL at the top. * indicates QTL detected in at least two subpopulations, + indicates QTL detected in at least two environments, and # indicates QTL detected in at least two environments and at least two subpopulations.

Trait	Chrom.	Peak start	Peak end	Subpopulation	Env.	σ^2 exp.	LOD score
Percent stalk lodged	1	46,588,740	49,621,514	B73PHJ40PHG47PHG84	Env4	0.90	7.37
Days to pollination	3	159,911,390	162,063,500	B73PHJ40LH82PHG47	Env2	0.79	6.45
Kernel size	4	194,976,668	218,848,123	B73PHG39LH82PHG47	Env1	0.54	6.25
Staygreen#	3	4,876,733	6,931,397	B73PHJ40LH82PHG84	Env3	0.72	6.05
Percent stalk lodged	5	3,782,663	7,767,736	B73PHG39LH82PHG47	Env3	0.58	5.76
Test weight	4	223,767,718	231,972,635	B73PHG39LH82PHG47	Env4	0.54	5.42
Kernel depth	8	13,598,724	16,770,910	PHJ40PHG39LH82PHG47	Env4	0.97	5.39
Ear width	1	94,367,655	97,817,457	PHJ40PHG39LH82PHG47	Env1	0.95	5.28
Leaf angle	5	198,211,350	206,468,542	B73PHJ40LH82PHG84	Env2	0.67	5.26
Staygreen	5	205,282,228	207,893,278	PHJ40PHG39LH82PHG84	Env3	0.53	5.25
Kernel size	10	135,059,714	138,592,814	B73PHJ40LH82PHG84	Env1	0.63	5.14
Plant height	4	188,413,296	227,273,408	PHJ40PHG39LH82PHG84	Env5	0.52	5.13
Rows per ear+	2	170,226,116	175,287,102	B73PHG39PHG47PHG84	Env4	0.54	5.10
Yield	5	169,762,617	172,023,995	B73PHG39PHG47PHG84	Env2	0.67	5.06
Staygreen#	9	23,257,240	34,027,035	B73PHG39PHG47PHG84	Env5	0.71	5.04
Staygreen	3	6,931,604	8,123,794	B73PHJ40LH82PHG84	Env5	0.65	5.01
Individual plant yield	5	169,762,617	172,023,995	B73PHG39PHG47PHG84	Env2	0.67	5.01
Percent root lodged	9	149,382,333	150,809,956	B73PHG39LH82PHG84	Env3	0.54	4.90
Kernel size	7	158,932,442	158,940,716	B73PHG39LH82PHG47	Env1	0.51	4.74
Upper stem diameter	8	121,799,125	145,698,118	PHJ40PHG39PHG47PHG84	Env4	0.66	4.62
Kernels per row	1	33,630,270	41,436,918	B73PHJ40PHG47PHG84	Env4	0.76	4.62
Kernels per row+	7	121,296,628	123,589,743	PHJ40PHG39PHG47PHG84	Env3	0.65	4.56
Tassel weight	1	41,469,416	46,581,002	B73PHJ40PHG47PHG84	Env4	0.75	4.56

Table A 5. (cont.)

Trait	Chrom.	Peak start	Peak end	Subpopulation	Env.	σ^2 exp.	LOD score
Percent stalk lodged	7	173,176,208	173,950,057	B73PHG39LH82PHG47	Env2	0.47	4.50
Anthesis-silking interval	8	164,358,589	165,171,215	B73PHG39LH82PHG84	Env1	0.49	4.48
Upper stem diameter	9	108,509,221	124,022,322	B73PHG39LH82PHG84	Env4	0.45	4.47
Days to pollination	7	78,786,414	79,011,543	B73PHG39LH82PHG47	Env2	0.51	4.39
Test weight	5	204,266,355	204,628,864	B73PHJ40LH82PHG47	Env1	0.70	4.39
Rows per ear+	8	123,533,960	136,399,657	B73PHG39PHG47PHG84	Env4	0.46	4.33
Individual plant yield+	8	112,979,261	116,850,356	PHJ40PHG39LH82PHG47	Env3	0.47	4.33
Kernels per row+	7	121,296,628	123,589,743	PHJ40PHG39PHG47PHG84	Env4	0.63	4.33
Leaf area to produce 1 g grain	10	136,475,818	139,839,300	PHJ40PHG39LH82PHG47	Env4	0.47	4.32
Kernels per plant	10	4,019,721	5,119,145	B73PHG39PHG47PHG84	Env1	0.65	4.32
Ear height	7	128,375,096	135,507,329	B73PHG39LH82PHG47	Env3	0.45	4.29
Kernels per plant	2	24,662,168	27,126,130	B73PHG39PHG47PHG84	Env3	0.46	4.28
Kernels per plant	6	149,719,245	153,268,083	B73PHG39LH82PHG84	Env2	0.46	4.28
Days to silking	7	138,593,498	153,717,605	B73PHG39LH82PHG47	Env2	0.45	4.24
Ear width	9	23,531,001	43,680,550	PHJ40PHG39LH82PHG47	Env1	0.48	4.22
Zipper effect	6	84,385,373	89,125,014	B73PHJ40PHG47PHG84	Env3	0.73	4.22
Percent stalk lodged	1	49,725,332	53,164,450	B73PHJ40PHG47PHG84	Env5	0.73	4.20
Ear width	2	25,089,630	32,588,036	B73PHG39PHG47PHG84	Env3	0.45	4.19
Days to pollination	3	154,648,059	159,871,976	B73PHJ40LH82PHG47	Env1	0.64	4.19
Kernel width	4	186,165,792	218,848,123	B73PHG39LH82PHG47	Env1	0.41	4.18
Tassel branch number	6	95,072,304	96,566,210	B73PHG39LH82PHG84	Env1	0.46	4.18
Kernels per plant	4	191,642,426	193,504,343	PHJ40PHG39LH82PHG47	Env2	0.46	4.14
Plant height	5	214,285,616	214,287,212	PHJ40PHG39LH82PHG47	Env4	0.93	4.14
Plant height	7	146,768,990	162,989,065	PHJ40PHG39LH82PHG47	Env4	0.93	4.14
Kernel length*	4	195,962,414	216,607,762	B73PHG39LH82PHG47	Env1	0.40	4.13
Upper stem diameter	7	162,031,530	162,976,433	B73PHG39LH82PHG47	Env1	0.45	4.13

Table A 5. (cont.)

Trait	Chrom.	Peak start	Peak end	Subpopulation	Env.	σ^2 exp.	LOD score
Ear width	7	3,562,178	4,801,428	B73PHJ40LH82PHG84	Env1	0.55	4.13
Staygreen	5	14,102,378	15,146,808	B73PHG39LH82PHG47	Env5	0.44	4.10
Percent barren plants	1	65,620,469	85,898,547	B73PHG39LH82PHG47	Env2	0.46	4.10
Plant height	1	227,452,177	237,055,557	B73PHG39LH82PHG47	Env5	0.43	4.08
Tassel weight	6	360,234	4,438,816	PHJ40PHG39PHG47PHG84	Env4	0.65	4.07
Kernel depth	6	632,147	5,065,426	B73PHG39PHG47PHG84	Env2	0.63	4.06
Zipper effect	6	115,297,526	118,074,674	B73PHJ40PHG47PHG84	Env2	0.76	4.05
Days to canopy closure	10	144,453,384	146,396,911	PHJ40PHG39LH82PHG47	Env4	0.49	4.04
Leaf angle	5	168,871,707	188,755,845	B73PHJ40LH82PHG84	Env2	0.55	4.04
Upper stem diameter	1	1,195,294	5,529,666	PHJ40PHG39PHG47PHG84	Env5	0.93	4.01
Upper stem diameter	7	147,527,941	160,589,463	PHJ40PHG39PHG47PHG84	Env5	0.93	4.01
Test weight	6	162,109,236	162,739,859	B73PHG39LH82PHG84	Env5	0.43	3.98
Days to silking	7	78,786,414	79,011,543	B73PHG39LH82PHG47	Env2	0.48	3.96
Anthesis-silking interval	3	143,802,648	150,835,942	B73PHG39LH82PHG47	Env2	0.43	3.95
Test weight	5	68,028,123	111,997,150	B73PHG39LH82PHG47	Env4	0.41	3.94
Staygreen	7	805,767	1,449,976	B73PHG39PHG47PHG84	Env4	0.62	3.94
Days to silking+	7	92,623,697	112,538,338	B73PHG39LH82PHG47	Env1	0.42	3.92
Total spike length	10	142,168,323	142,798,590	B73PHG39LH82PHG47	Env4	0.43	3.92
Rows per ear	2	24,033,087	28,315,770	B73PHG39PHG47PHG84	Env3	0.44	3.90
Zipper effect	10	115,705,447	138,592,814	B73PHJ40LH82PHG84	Env1	0.53	3.89
Days to silking	3	159,870,918	162,063,500	B73PHJ40LH82PHG47	Env2	0.61	3.87
Fill length	1	33,630,270	41,436,918	B73PHJ40PHG47PHG84	Env4	0.70	3.87
Ear width	8	121,798,063	131,125,755	PHJ40PHG39LH82PHG84	Env4	0.44	3.86
Plant height#	6	88,998,027	91,874,104	B73PHG39PHG47PHG84	Env1	0.42	3.84
Ear length	7	3,886,738	5,534,435	B73PHG39LH82PHG84	Env1	0.45	3.84
Test weight	9	23,257,240	34,027,035	B73PHG39PHG47PHG84	Env5	0.61	3.84
Individual plant yield	8	111,704,703	114,742,778	PHJ40PHG39LH82PHG47	Env5	0.46	3.82

Table A 5. (cont.)

Trait	Chrom.	Peak start	Peak end	Subpopulation	Env.	σ^2 exp.	LOD score
Leaf angle	4	10,032,488	22,107,783	PHJ40PHG39PHG47PHG84	Env4	0.59	3.82
Days to pollination	4	156,970,331	163,201,517	B73PHJ40PHG47PHG84	Env2	0.69	3.82
Kernel width*	7	1,788,983	5,613,819	PHJ40PHG39LH82PHG47	Env3	0.89	3.82
Kernel width*	8	23,889,002	39,123,138	PHJ40PHG39LH82PHG47	Env3	0.89	3.82
Kernels per plant	6	780,023	9,147,734	B73PHJ40PHG47PHG84	Env4	0.74	3.81
Est. total leaf area	5	10,009,509	10,937,056	PHJ40PHG39LH82PHG47	Env4	0.44	3.80
Percent stalk lodged	3	2,524,737	4,542,475	B73PHG39PHG47PHG84	Env2	0.56	3.79
Plant height	1	289,275,498	290,819,704	B73PHG39PHG47PHG84	Env1	0.58	3.79
Rows per ear+	2	151,702,733	175,287,102	B73PHG39PHG47PHG84	Env3	0.44	3.78
Kernels per plant	1	225,879,718	246,398,685	B73PHJ40LH82PHG47	Env1	0.62	3.78
Anthesis-silking interval#	9	148,059,470	151,367,667	B73PHJ40LH82PHG47	Env3	0.62	3.78
Anthesis-silking interval*	3	184,454,286	204,578,999	B73PHG39LH82PHG84	Env2	0.41	3.77
Staygreen	4	513,375	2,409,503	B73PHG39PHG47PHG84	Env4	0.58	3.77
Rows per ear	2	47,515,667	60,273,128	B73PHG39PHG47PHG84	Env3	0.43	3.76
Plant height#	6	88,998,027	95,316,577	B73PHG39PHG47PHG84	Env2	0.43	3.76
Ear width	9	116,244,357	140,845,426	PHJ40PHG39LH82PHG47	Env1	0.45	3.74
Staygreen#	4	180,911,155	190,376,044	B73PHG39PHG47PHG84	Env5	0.56	3.73
Staygreen	8	171,745,601	172,674,842	B73PHG39PHG47PHG84	Env2	0.56	3.72
Days to pollination	1	289,275,498	290,687,102	B73PHG39PHG47PHG84	Env1	0.56	3.72
Ear width	10	79,032,870	117,466,348	B73PHG39LH82PHG47	Env2	0.40	3.71
Percent stalk lodged	3	179,264,991	193,759,637	PHJ40PHG39LH82PHG47	Env2	0.88	3.71
Kernels per plant	7	123,480,196	143,750,751	PHJ40PHG39PHG47PHG84	Env4	0.57	3.70
Days to canopy closure	2	191,151,390	192,786,597	B73PHG39LH82PHG47	Env3	0.41	3.67
Leaf angle	5	14,588,986	15,332,090	B73PHG39LH82PHG47	Env2	0.41	3.65
Total spike length	4	13,396,339	13,417,698	B73PHG39PHG47PHG84	Env1	0.45	3.65
Kernel width*	7	1,788,983	5,613,819	PHJ40PHG39PHG47PHG84	Env3	0.91	3.65
Kernel width*	8	23,889,002	39,123,138	PHJ40PHG39PHG47PHG84	Env3	0.91	3.65

Table A 5. (cont.)

Trait	Chrom.	Peak start	Peak end	Subpopulation	Env.	σ^2 exp.	LOD score
Leaf area to produce 1 g grain	4	130,908,636	147,915,662	B73PHG39LH82PHG47	Env1	0.37	3.64
Kernel depth	4	232,927,892	233,636,242	B73PHG39LH82PHG47	Env1	0.37	3.64
Staygreen	5	194,560,141	203,043,846	PHJ40PHG39PHG47PHG84	Env1	0.57	3.64
Upper stem diameter	4	181,445,900	187,547,034	B73PHG39LH82PHG47	Env2	0.37	3.63
Staygreen#	3	4,190,244	5,325,919	B73PHG39LH82PHG47	Env3	0.39	3.62
Ear height	7	2,774,194	3,484,486	PHJ40PHG39LH82PHG47	Env2	0.43	3.62
Leaf angle	5	80,807,149	92,242,189	B73PHJ40LH82PHG84	Env2	0.52	3.61
Kernels per plant	9	479,678	6,851,809	B73PHJ40LH82PHG47	Env3	0.62	3.61
Zipper effect	7	6,069,495	6,145,700	B73PHJ40PHG47PHG84	Env2	0.72	3.61
Individual plant yield	1	85,989,818	115,219,132	B73PHG39LH82PHG47	Env2	0.41	3.60
Kernel width	2	175,093,157	185,014,419	B73PHG39LH82PHG84	Env4	0.41	3.60
Fill length	7	123,480,196	143,750,751	PHJ40PHG39PHG47PHG84	Env4	0.56	3.58
Days to silking	7	169,841,708	176,549,717	PHJ40PHG39LH82PHG47	Env2	0.91	3.58
Days to canopy closure	9	1,000,101	3,137,210	B73PHG39LH82PHG84	Env2	0.41	3.57
Fill length	1	68,933,365	85,898,547	B73PHG39PHG47PHG84	Env2	0.42	3.57
Upper stem diameter	4	3,460,707	4,737,309	B73PHG39LH82PHG84	Env3	0.43	3.55
Days to pollination	9	140,349,197	141,408,199	B73PHG39LH82PHG84	Env3	0.42	3.54
Days to pollination	2	3,864,775	4,370,073	PHJ40PHG39LH82PHG84	Env3	0.42	3.53
Ear length	1	55,068,362	78,216,166	B73PHG39PHG47PHG84	Env4	0.42	3.53
Anthesis-silking interval	6	166,182,608	169,082,827	B73PHG39LH82PHG47	Env2	0.41	3.52
Kernel size+	1	10,821,326	11,950,330	PHJ40PHG39LH82PHG47	Env2	0.43	3.51
Ear width	4	41,890,422	60,810,258	PHJ40PHG39PHG47PHG84	Env1	0.55	3.51
Ear height#	3	10,064,861	30,451,257	B73PHJ40PHG47PHG84	Env5	0.66	3.51
Total spike length	2	15,133,959	18,308,566	B73PHG39PHG47PHG84	Env1	0.41	3.50
Kernels per plant	8	135,458,018	148,264,087	B73PHG39PHG47PHG84	Env3	0.41	3.49
Anthesis-silking interval	3	18,636,348	21,368,908	B73PHG39LH82PHG47	Env3	0.41	3.49
Days to canopy closure	7	147,159,672	149,564,697	PHJ40PHG39LH82PHG84	Env2	0.39	3.47

Table A 5. (cont.)

Trait	Chrom.	Peak start	Peak end	Subpopulation	Env.	σ^2 exp.	LOD score
Staygreen	1	191,858,466	206,505,340	PHJ40PHG39LH82PHG84	Env1	0.39	3.47
Test weight	4	180,911,155	190,376,044	B73PHG39PHG47PHG84	Env5	0.53	3.47
Anthesis-silking interval	9	11,298,531	13,663,338	PHJ40PHG39LH82PHG84	Env1	0.39	3.46
Yield	1	85,989,818	115,219,132	B73PHG39LH82PHG47	Env2	0.39	3.45
Leaf angle	5	65,224,459	80,393,777	B73PHJ40LH82PHG84	Env2	0.51	3.45
Days to canopy closure	1	298,298,446	301,252,677	B73PHG39PHG47PHG84	Env1	0.53	3.44
Ear height#	3	26,928,916	58,722,938	B73PHG39LH82PHG47	Env1	0.41	3.43
Percent stalk lodged	3	228,720,407	229,646,236	B73PHG39LH82PHG84	Env4	0.43	3.43
Tassel branch number	1	47,993,756	50,779,930	B73PHG39LH82PHG47	Env4	0.38	3.42
Kernel length	2	2,321,924	4,263,380	B73PHG39LH82PHG84	Env4	0.39	3.42
Tassel branch number	8	162,551,928	168,935,094	PHJ40PHG39LH82PHG84	Env1	0.39	3.41
Days to canopy closure	10	139,840,256	142,358,624	PHJ40PHG39LH82PHG47	Env4	0.40	3.41
Kernel length	6	147,917,479	150,887,726	B73PHG39LH82PHG84	Env1	0.42	3.41
Rows per ear	2	64,394,765	97,422,086	B73PHG39PHG47PHG84	Env3	0.41	3.40
Rows per ear	2	124,058,882	148,716,086	B73PHG39PHG47PHG84	Env3	0.41	3.40
Rows per ear+	8	123,533,960	147,718,493	B73PHG39PHG47PHG84	Env3	0.40	3.39
Days to silking+	9	136,916,332	140,949,805	B73PHG39LH82PHG84	Env3	0.41	3.39
Yield	9	151,249,835	155,721,479	B73PHG39PHG47PHG84	Env4	0.54	3.39
Tassel weight	9	148,260,972	149,725,727	PHJ40PHG39PHG47PHG84	Env1	0.56	3.39
Kernel width	5	192,230,662	204,548,811	B73PHJ40LH82PHG47	Env1	0.58	3.39
Fill length	4	166,347,536	171,053,526	PHJ40PHG39LH82PHG84	Env4	0.38	3.37
Est. total leaf area	3	35,878,953	56,284,547	B73PHJ40LH82PHG84	Env4	0.49	3.33
Total spike length	4	234,305,557	237,679,895	PHJ40PHG39PHG47PHG84	Env2	0.54	3.33
Ear length	3	179,264,991	190,569,861	PHJ40PHG39PHG47PHG84	Env2	0.89	3.33
Ear length	4	2,482,986	14,692,315	PHJ40PHG39PHG47PHG84	Env2	0.89	3.33
Ear height	5	151,317,461	176,114,983	PHJ40PHG39PHG47PHG84	Env5	0.57	3.32
Tassel weight	4	28,771,743	37,018,267	B73PHG39LH82PHG84	Env2	0.37	3.31

Table A 5. (cont.)

Trait	Chrom.	Peak start	Peak end	Subpopulation	Env.	σ^2 exp.	LOD score
Ear height	7	41,688,322	79,011,543	B73PHG39LH82PHG47	Env3	0.37	3.30
Plant height#	6	75,620,093	92,327,477	B73PHG39LH82PHG47	Env2	0.37	3.29
Staygreen	2	208,653,738	220,321,877	B73PHJ40LH82PHG47	Env2	0.57	3.29
Leaf angle	1	3,078,660	3,886,207	PHJ40PHG39LH82PHG84	Env3	0.37	3.28
Anthesis-silking interval	2	23,876,209	29,231,750	B73PHG39LH82PHG84	Env1	0.39	3.28
Rows per ear	6	153,759,415	159,117,819	B73PHG39PHG47PHG84	Env4	0.39	3.28
Percent stalk lodged	7	5,273,157	5,324,073	B73PHG39LH82PHG47	Env3	0.40	3.28
Kernel length	7	173,888,618	175,642,308	B73PHG39LH82PHG47	Env2	0.41	3.28
Rows per ear	2	99,178,158	122,234,005	B73PHG39PHG47PHG84	Env3	0.39	3.27
Kernel depth	10	135,998,095	138,262,102	B73PHJ40LH82PHG84	Env1	0.47	3.27
Ear height	10	141,564,614	144,914,233	B73PHG39PHG47PHG84	Env4	0.51	3.26
Ear length	5	214,285,616	214,287,212	PHJ40PHG39LH82PHG47	Env2	0.88	3.26
Ear length	7	146,768,990	162,989,065	PHJ40PHG39LH82PHG47	Env2	0.88	3.26
Kernels per plant	4	179,617,154	191,765,208	PHJ40PHG39LH82PHG47	Env1	0.38	3.25
Rows per ear+	2	187,442,850	207,970,060	B73PHG39PHG47PHG84	Env2	0.38	3.24
Ear width	3	209,130,373	216,246,373	PHJ40PHG39PHG47PHG84	Env3	0.53	3.24
Test weight	8	21,699,850	25,348,389	PHJ40PHG39PHG47PHG84	Env3	0.52	3.22
Individual plant yield	10	1,946,154	4,676,203	PHJ40PHG39PHG47PHG84	Env3	0.54	3.22
Anthesis-silking interval	1	184,118,971	200,716,028	B73PHG39LH82PHG84	Env1	0.36	3.21
Rows per ear	2	209,507,114	223,172,507	B73PHG39LH82PHG84	Env4	0.36	3.21
Est. total leaf area	8	5,329,743	8,887,533	B73PHG39PHG47PHG84	Env1	0.50	3.20
Zipper effect	8	164,151,396	164,377,005	B73PHJ40PHG47PHG84	Env2	0.65	3.20
Leaf angle	7	125,506,402	130,703,839	PHJ40PHG39LH82PHG84	Env4	0.37	3.18
Upper stem diameter	3	35,878,953	56,284,547	B73PHJ40LH82PHG84	Env4	0.47	3.18
Days to silking+	9	136,916,332	140,773,678	B73PHG39LH82PHG84	Env4	0.39	3.17
Kernels per plant	2	170,226,116	175,287,102	B73PHG39PHG47PHG84	Env4	0.39	3.17
Kernel depth	5	196,407,823	203,043,846	PHJ40PHG39PHG47PHG84	Env1	0.52	3.17

Table A 5. (cont.)

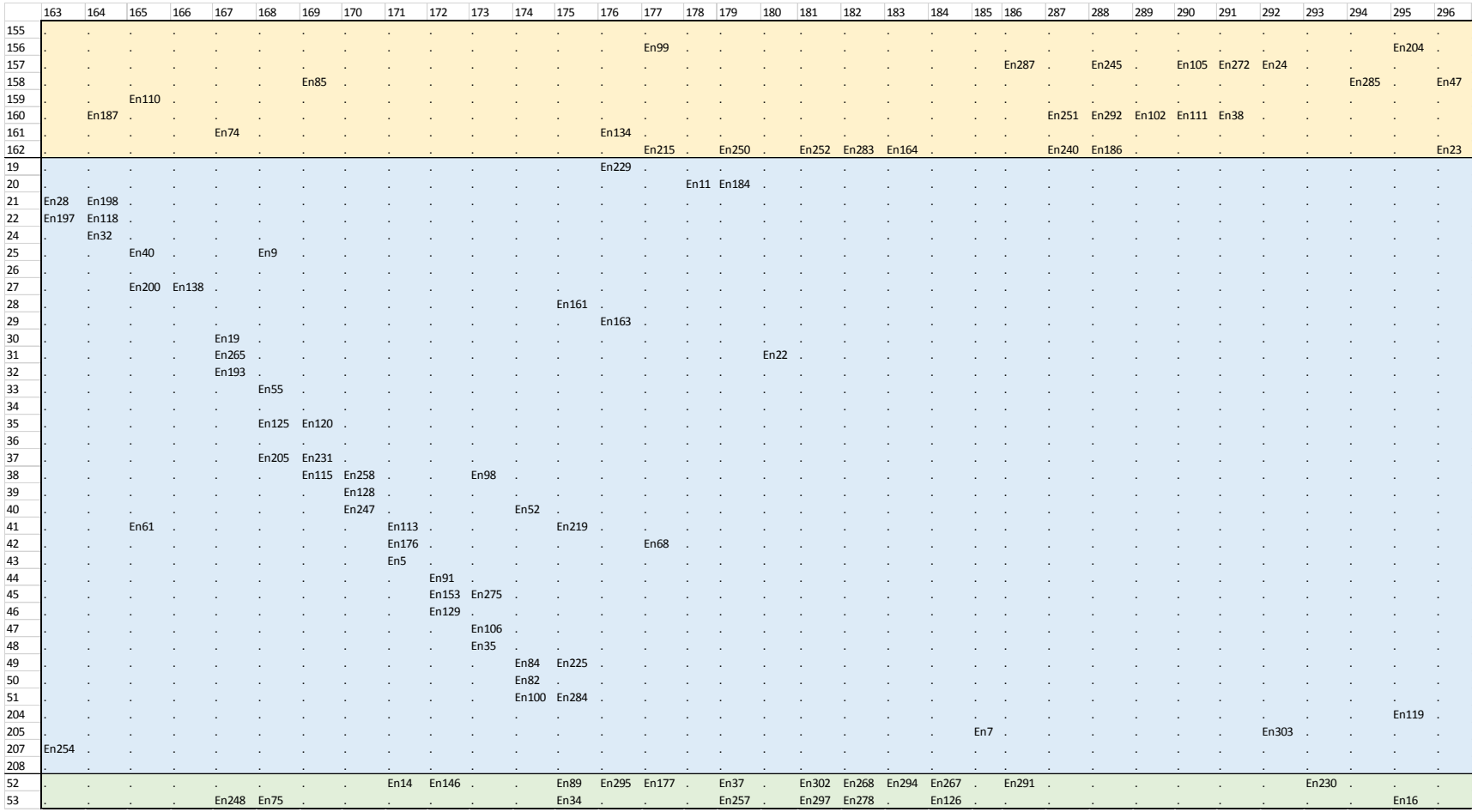
Trait	Chrom.	Peak start	Peak end	Subpopulation	Env.	σ^2 exp.	LOD score
Upper stem diameter	5	206,272,762	212,818,851	B73PHG39LH82PHG84	Env4	0.37	3.16
Staygreen#	4	174,778,938	190,406,861	B73PHG39LH82PHG47	Env3	0.39	3.15
Lower stem diameter	9	108,509,221	124,022,322	B73PHG39PHG47PHG84	Env2	0.36	3.14
Kernel width	2	18,309,047	23,981,749	B73PHG39LH82PHG47	Env3	0.36	3.14
Days to silking+	7	92,623,697	112,538,338	B73PHG39LH82PHG47	Env2	0.35	3.13
Ear height	9	136,916,332	140,348,897	B73PHG39LH82PHG84	Env5	0.37	3.13
Leaf area to produce 1 g grain	1	292,085,515	294,084,982	B73PHG39PHG47PHG84	Env3	0.38	3.13
Percent stalk lodged	1	30,685,708	36,831,426	PHJ40PHG39LH82PHG47	Env3	0.39	3.13
Yield	7	19,083,475	28,818,009	PHJ40PHG39PHG47PHG84	Env4	0.51	3.13
Anthesis-silking interval	5	196,407,823	202,818,540	PHJ40PHG39PHG47PHG84	Env3	0.51	3.10
Tassel weight	2	167,010,884	188,152,844	PHJ40PHG39PHG47PHG84	Env4	0.51	3.10
Plant height	4	178,582,304	187,413,078	PHJ40PHG39LH82PHG84	Env4	0.36	3.08
Test weight	2	11,754,560	15,117,883	B73PHG39PHG47PHG84	Env2	0.38	3.08
Kernel size	3	217,280,325	229,900,231	B73PHG39LH82PHG84	Env3	0.40	3.08
Days to pollination#	5	196,407,823	202,818,540	PHJ40PHG39PHG47PHG84	Env1	0.51	3.08
Individual plant yield	9	150,006,975	155,721,479	B73PHG39PHG47PHG84	Env4	0.51	3.08
Staygreen#	9	23,531,001	45,379,465	B73PHJ40LH82PHG47	Env2	0.53	3.08
Staygreen	10	110,622,527	126,869,661	B73PHG39PHG47PHG84	Env4	0.36	3.07
Tassel branch number	8	104,624,572	116,850,356	PHJ40PHG39LH82PHG47	Env3	0.37	3.07
Tassel weight	9	127,467,979	138,240,196	PHJ40PHG39PHG47PHG84	Env1	0.52	3.06
Ear height	7	34,681,075	40,379,142	B73PHG39LH82PHG47	Env3	0.36	3.05
Anthesis-silking interval#	9	150,006,975	156,437,290	B73PHG39PHG47PHG84	Env2	0.49	3.05
Plant height	5	188,660,783	205,791,801	B73PHJ40LH82PHG84	Env1	0.46	3.04
Test weight	4	10,280,585	22,552,418	PHJ40PHG39PHG47PHG84	Env3	0.52	3.04
Ear height	4	233,543,148	236,185,077	PHJ40PHG39LH82PHG84	Env5	0.34	3.02
Individual plant yield	4	233,543,148	236,185,077	PHJ40PHG39LH82PHG84	Env5	0.34	3.02
Plant height	9	564,150	4,958,541	B73PHJ40LH82PHG47	Env3	0.56	2.99

Table A 5. (cont.)

Trait	Chrom.	Peak start	Peak end	Subpopulation	Env.	σ^2 exp.	LOD score
Kernel length	3	195,644,839	201,093,147	B73PHG39LH82PHG47	Env2	0.34	2.96
Leaf area to produce 1 g grain	1	122,474,601	161,534,021	B73PHG39LH82PHG47	Env1	0.36	2.95
Zipper effect	2	9,414,414	11,398,947	B73PHJ40PHG47PHG84	Env2	0.60	2.95
Days to silking	5	162,838,592	178,828,400	B73PHJ40LH82PHG84	Env2	0.43	2.93
Kernel width	6	111,767,135	132,226,419	B73PHJ40LH82PHG84	Env1	0.46	2.93
Staygreen	10	135,059,714	141,589,366	B73PHJ40LH82PHG84	Env2	0.43	2.91
Kernel size	9	479,649	1,680,246	PHJ40PHG39LH82PHG47	Env1	0.39	2.89
Leaf angle	7	152,019,560	156,738,754	B73PHG39PHG47PHG84	Env2	0.49	2.88
Kernel length	4	182,639,219	190,376,044	B73PHJ40PHG47PHG84	Env1	0.59	2.88
Kernel length*	4	190,385,663	212,217,200	B73PHJ40PHG47PHG84	Env1	0.59	2.88
Ear width	1	17,679,622	23,249,704	PHJ40PHG39LH82PHG84	Env3	0.33	2.87
Percent stalk lodged	7	2,586,167	2,997,697	B73PHG39LH82PHG47	Env3	0.36	2.86
Days to silking	1	41,098,315	54,821,530	B73PHG39LH82PHG47	Env2	0.33	2.85
Yield	3	7,982,019	30,141,889	B73PHJ40PHG47PHG84	Env5	0.60	2.82
Kernel width	10	135,059,714	145,283,427	B73PHJ40LH82PHG84	Env1	0.42	2.80
Rows per ear	3	166,206,516	181,364,801	B73PHG39PHG47PHG84	Env4	0.48	2.80
Kernel size+	1	5,518,212	11,112,099	PHJ40PHG39LH82PHG47	Env1	0.35	2.79
Zipper effect	7	133,562,976	138,459,755	PHJ40PHG39LH82PHG84	Env2	0.33	2.78
Leaf angle	3	10,064,861	30,451,257	PHJ40PHG39PHG47PHG84	Env1	0.47	2.78
Leaf area to produce 1 g grain	5	14,102,378	25,792,179	B73PHG39LH82PHG84	Env2	0.33	2.75
Leaf angle	4	198,118,695	206,869,576	B73PHG39LH82PHG47	Env4	0.32	2.72
Ear length	4	237,680,133	237,875,000	PHJ40PHG39PHG47PHG84	Env2	0.46	2.71
Days to pollination	5	162,838,592	188,660,194	B73PHJ40LH82PHG84	Env2	0.42	2.70
Tassel weight	4	6,243,660	10,656,413	B73PHG39LH82PHG84	Env2	0.33	2.69
Plant height	3	10,064,861	30,451,257	B73PHJ40PHG47PHG84	Env5	0.56	2.69
Ear height	7	5,324,073	13,844,998	B73PHG39LH82PHG47	Env3	0.33	2.65
Kernels per plant	9	148,200,059	153,165,449	B73PHJ40LH82PHG47	Env3	0.47	2.49

Table A 5. (cont.)

Trait	Chrom.	Peak start	Peak end	Subpopulation	Env.	σ^2 exp.	LOD score
Leaf angle	1	17,679,622	23,249,704	PHJ40PHG39LH82PHG84	Env3	0.29	2.48
Kernel depth	4	138,153,170	160,562,238	B73PHG39LH82PHG47	Env1	0.27	2.44
Kernel depth	4	66,284,950	71,152,611	B73PHG39LH82PHG47	Env1	0.29	2.36
Days to pollination#	5	198,211,350	208,641,184	B73PHJ40LH82PHG84	Env2	0.35	2.26
Anthesis-silking interval*	3	201,673,692	202,040,219	B73PHG39LH82PHG47	Env2	0.26	2.07
Ear height	7	153,831,662	167,589,993	B73PHG39LH82PHG47	Env3	0.27	2.02
Rows per ear+	2	189,543,976	211,522,624	B73PHG39PHG47PHG84	Env4	0.23	1.78
Kernel depth	4	122,832,418	136,253,505	B73PHG39LH82PHG47	Env1	0.21	1.77



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155																																		
156															En99																		En204	
157																								En287		En245		En105	En272	En24				
158							En85																									En285		En47
159			En110																															
160		En187																							En251	En292	En102	En111	En38					
161					En74									En134																				
162															En215		En250		En252	En283	En164				En240	En186								En23
19														En229																				
20																En11	En184																	
21	En28	En198																																
22	En197	En118																																
24		En32																																
25			En40			En9																												
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27			En200	En138																														
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36																																		
37						En205	En231																											
38							En115	En258			En98																							
39								En128																										
40								En247				En52																						
41			En61						En113				En219																					
42									En176						En68																			
43									En5																									
44										En91																								
45										En153	En275																							
46										En129																								
47											En106																							
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53					En248	En75							En34				En257		En297	En278		En126											En16	

Figure A 1. The x-axis represents the 171 NSS RIL and DH inbreds and the y-axis represents the 46 SSS RIL and DH inbreds that were used to create the 320 testcross hybrids. The three horizontally divided sections show the SSS subpopulations (from top to bottom, across all pages) PHJ40xPHG39, B73xPHG39, and PHJ40xB73. The first page consists of crosses with PHG47xPHG84 inbreds serving as the NSS parents, while the second and third pages show LH82xPHG47 inbreds serving as the NSS parents, and the fourth and fifth pages show LH82xPHG84 inbreds as the NSS parents. Each hybrid was coded as an entry, signified as "En" followed by a number 0-320.

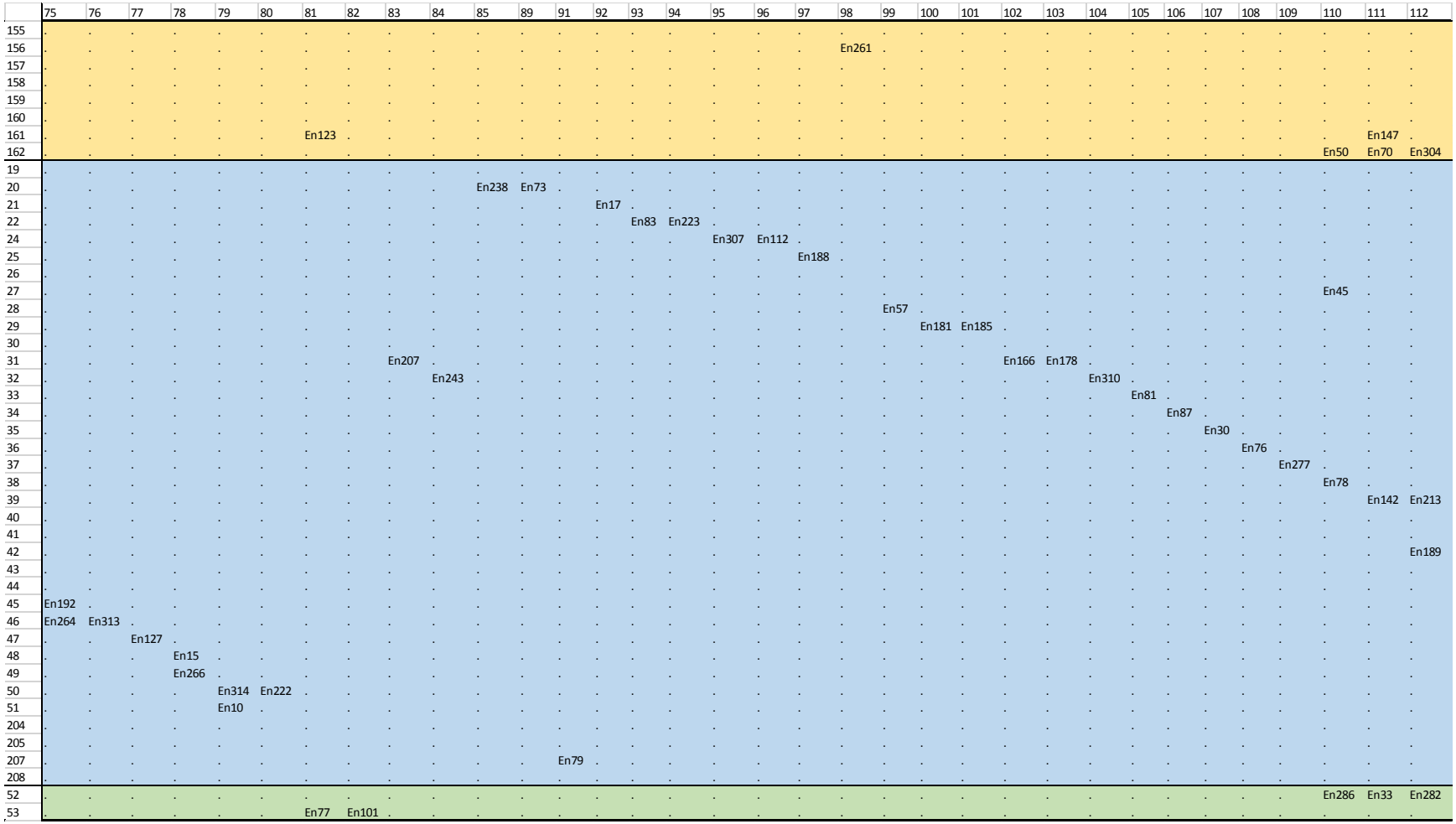
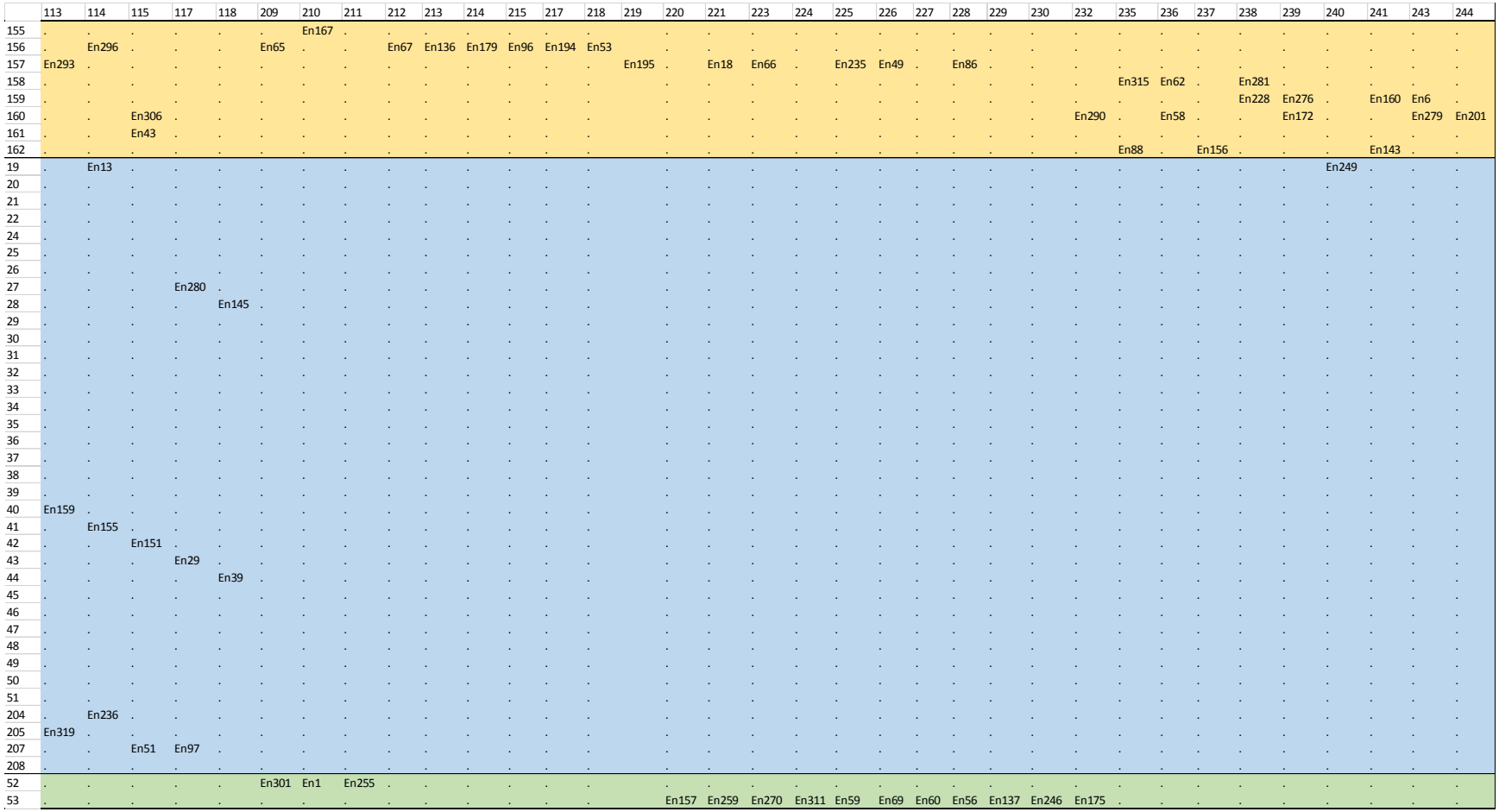


Figure A 1. (cont.)



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155	.	.	.	.	.	.	En167	.	.	.	.	.	.	.		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
156	.	En296	.	.	.	En65	.	.	En67	En136	En179	En96	En194	En53		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
157	En293	.	.	.	.	.	.	.	.	.	.	.	.	.	En195	.	En18	En66	.	En235	En49	.	En86	.	.	.	.	.	.	.	.	.	.	.	.	.
158	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	En315	En62	.	En281	.	.	.	.	.
159	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	En228	En276	.	En160	En6	.
160	.	.	En306	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	En290	.	En58	.	.	En172	.	.	En279	En201
161	.	.	En43	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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19	.	En13	.	.	.	.	.	.	.	.	.	.	.	.		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	En249	.	.	.
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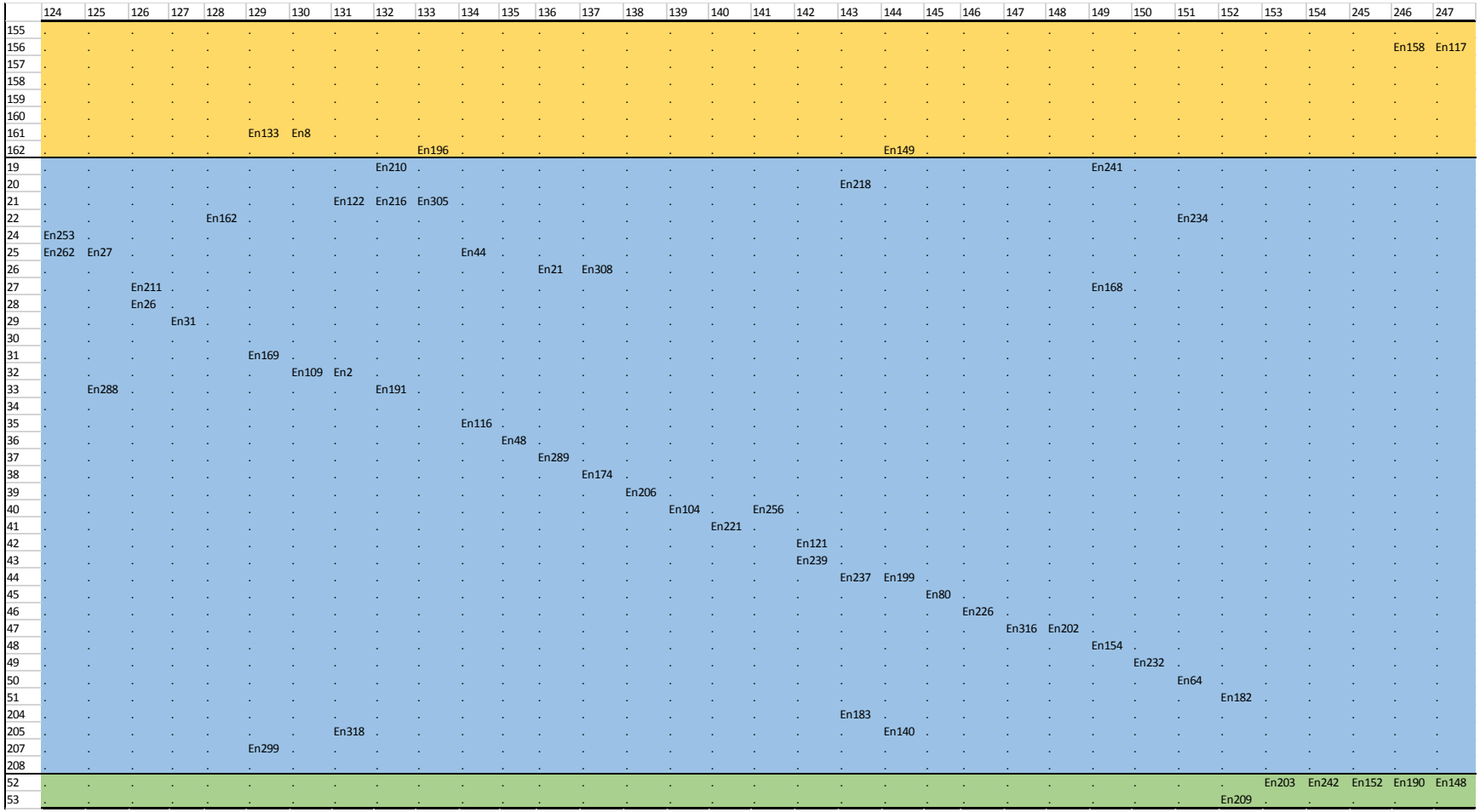
Figure A 1. (cont.)



	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	245	246	247
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161						En133	En8																											
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20																				En218														
21								En122	En216	En305																									
22					En162																							En234						
24	En253																																	
25	En262	En27									En44																							
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207						En299																												
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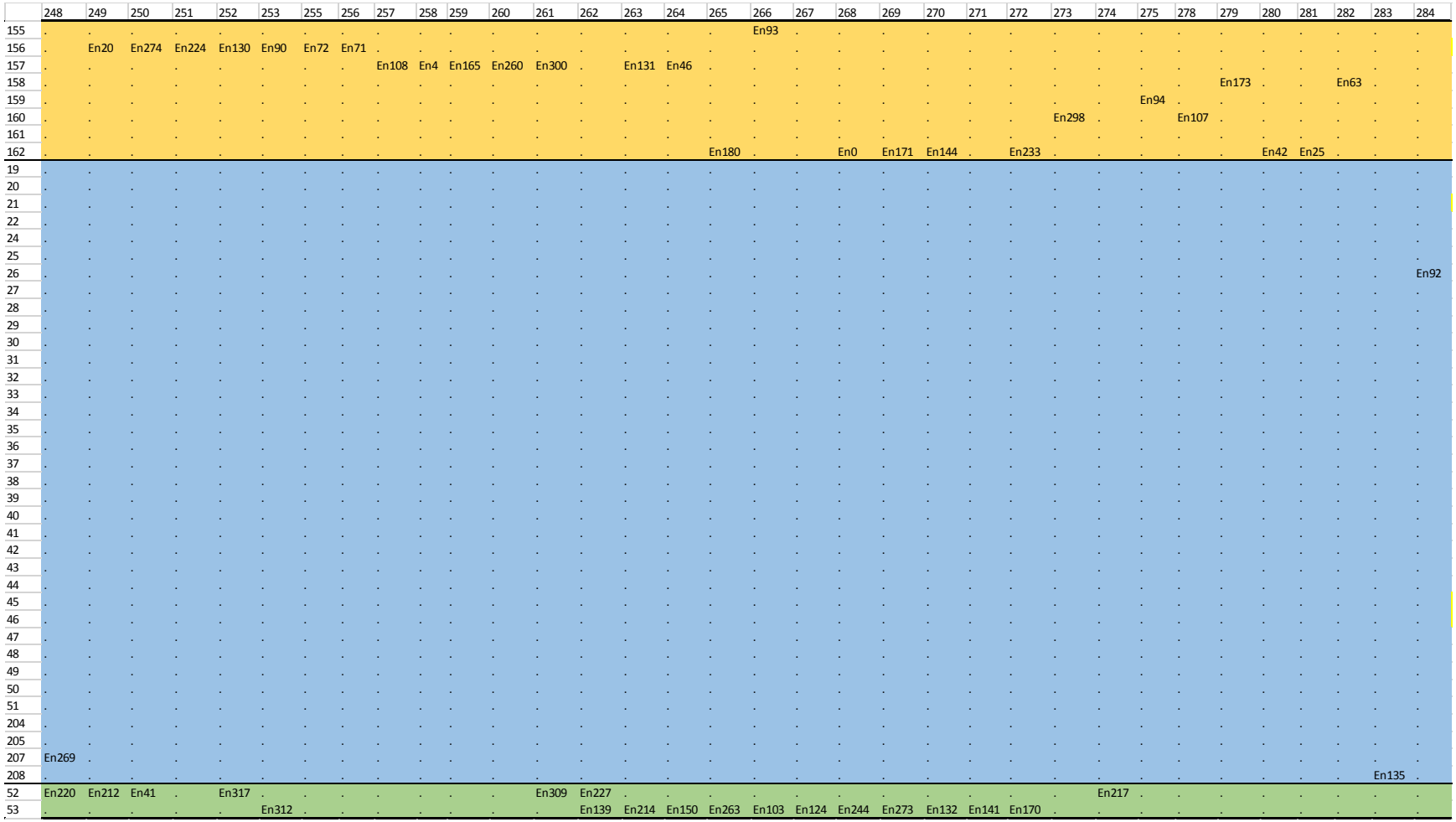
52																														En203	En242	En152	En190	En148
53																													En209					

Figure A 1. (cont.)



	248	249	250	251	252	253	255	256	257	258	259	260	261	262	263	264	265	266	267	268	269	270	271	272	273	274	275	278	279	280	281	282	283	284
155																		En93																
156		En20	En274	En224	En130	En90	En72	En71																										
157									En108	En4	En165	En260	En300		En131	En46																		
158																													En173			En63		
159																											En94							
160																									En298			En107						
161																																		
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Figure A 1. (cont.)

Figure A 2. Variability between different genotypes as shown by ears of three different genotypes (upper left), by ear leaves of two different genotypes (upper right), and by staygreen exhibited by two different genotypes (bottom).

Figure A 3. Drought stress resulted in leaf rolling. Some genotypes were significantly affected, while others showed comparatively lesser leaf rolling.