QTL Mapping of Panicle Architecture and Yield-related Traits Between Two U.S. Rice Cultivars ‘LaGrue’ and ‘Lemont’

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QTL Mapping of Panicle Architecture and Yield-Related Traits Between Two U.S. Rice Cultivars 'LaGrue' and 'Lemont'

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Abbreviations:

HD, 50% Heading Date; FLL, Flag Leaf Length; FLW, Flag Leaf Width; PBN, Primary Branch Number; PH, PlantHeight; PL, Panicle Length; SBN, Secondary Branch Number.

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ABSTRACT

Grain yield is a quantitative trait that is determined by several agronomic traits. Unfortunately, there is little information about the genetics behind yield components in U.S. rice cultivars. The objective of the study were to 1) conduct a QTL study for identification of chromosome regions associated with yield traits in two US developed rice cultivars and 2) identify candidate genes in major QTL regions related to yield traits. Four rice cultivars were evaluated in the summer 2017 at the University of Arkansas System Division of Agriculture's Rice Research and Extension Center (RREC) at Stuttgart, AR for 15 agronomic traits associated with yield. Of the four cultivars, "LaGrue" had a higher number of seeds/panicle, number of primary panicle branches/panicle, and number of seeds/plant and "Lemont", despite having longer panicles and higher 100 seed weight/panicle, produced the least number of seeds among the cultivars. A bi-parental population was developed from a cross between LaGrue and Lemont for QTL analysis. Leaf samples from F_2 plants were collected for genetic analysis. A set of 322 $F_{2:3}$ lines were evaluated in a randomized complete block design (RCBD) for several agronomic traits at two locations with three replications for each line. A total of 17 major QTLs were detected including two major QTLs for plant height on chromosome 1 and two major QTLs for flag leaf length and panicle length on chromosome 8 with seven candidate genes found in these regions. The results from the study would be useful for marker assisted selection in rice breeding.

INTRODUCTION

Rice is one of the most important food crops in the world along with wheat and maize (IRRI 2019). About 140 million hectares of rice are harvested in the world annually. Approximately half of the world's population relies on rice as part of its diet (Ricepedia 2019). Human consumption of rice accounts for 85% of global production (IRRI, 2019). In the U.S., Arkansas is the top rice producing state accounting for about 48% of total U.S. rice production (Hardke 2018). Rice is one of the top three cash crops for Arkansas farmers, and in 2019 rice producers harvested about 1.126 million acres of rice (Hardke 2019).

Selecting for higher grain yield is one of the main objectives for public and private breeding programs in the U.S. and around the world. Grain yield is a complex quantitative trait consisting of multiple yield components (Xing et al. 2010). Yield components such as number of tillers/plant, number of panicles/plant, number of

seeds/panicle, and seed weight/panicle have been found to contribute to overall yield in rice cultivars (Devi et al. 2017; Samonte et al. 1998). Each yield component can be controlled by multiple genes that have a small effect on the phenotype and are greatly affected by the environment (Xing et al. 2010). Many QTL (quantitative trait locus) mapping studies have been done over the years searching for major QTL for use in breeding. Sun et al. (2017) found twelve QTLs for grain number, panicle length, number of primary panicle branches, and number of secondary branches on chr. 6 in four backcross populations between an indica hybrid restorer line 'HR1128' assigned as the donor parent and the japonica cultivar 'Nipponbare' the recurrent parent. Zhang et al. (2015) found two QTLs for panicle length on chr's 6 and 8 in four backcross populations resulting from the cross Nipponbare, the recurrent parent, and indica line 'WS3', the donor parent. They found that the QTL on chr.6 had a larger effect with longer panicles and increased number of primary and secondary branches than the QTL on chr. 8. Han et al. (2017) found five major QTLs for heading date and plant height under different day-length conditions using a RIL population derived from the indica line 'Zenshan 97' and japonica line 'Xizang 2'. Two major QTLs for heading date on chromosomes 7 and one on chromosome 8 were detected under long day conditions in all 3 years of the study along with major QTLs for plant height on chromosome 1 and 7 that were detected in all 3 years. Zhu et al. (2011) detected a QTL for panicle number on chr.1 using an introgression line "C3074" derived from a set of 112 CSSL lines that were developed from Nipponbare, as the donor parent, and indica line 'Guangluai 4" as the recurrent parent. The C3074 line had significantly fewer panicles compared to Guangluai 4. The QTL was fine mapped to a 34.4kb region on the long arm of chr. 1 and had an negative impact on panicle length, plant height, grain number per panicle, and grain yield per plant compared to Guangluai 4. Begum et al. (2015) found 52 QTLs for yield and other agronomic traits from a GWAS study of 369 elite breeding lines including a major QTL for flowering time on chromosome 3 and major QTL for grain length, width, and length-breadth ratio co-localized on chromosome 7. Another GWAS study by Zhang et al. (2019) using 150 rice landraces found QTL near known yield traits such as *SD-1, Hd1, Ghd7, and GW8*. To determine the genetics behind each yield component, a QTL mapping study was done to look for chromosomal regions linked to each yield component. Detecting major QTLs for yield traits that are stable across environments would allow researchers to find potential candidate genes that could be used for selection in rice breeding (Collard et al. 2005).

A QTL mapping study was done using a bi-parental population developed from a cross between 'LaGrue' and 'Lemont' to look for QTLs associated with panicle architecture and yield related traits. The objectives for this project are to; 1) conduct a parental yield study on four U.S. cultivars, LaGrue, Lemont, 'Bengal', 'Mars' to evaluate yield components between each cultivar and to determine which two varieties would be useful in developing a bi-parental population; 2) conduct a QTL mapping study on panicle architecture and other yield-related traits to detect major QTLs; and 3) identify candidate genes in the major QTL associated with yield traits. The study will provide useful information for breeders to select and develop high yield rice cultivars through marker-assisted selection in rice molecular breeding.

MATERIALS AND METHODS

Preliminary Yield Study

A preliminary study was conducted on four US developed *tropical japonica* cultivars, LaGrue (PI 568891) (Moldenhauer et al., 1994), Lemont (PI 475833) (Bollich et al. 1985), Bengal (PI 561735) (Linscombe et al. 1993), and Mars (Clor 9945) (Johnston et al. 1979) and the goal was to compare yield traits among the four cultivars and to determine which cultivars should be used in the development of a bi-parental population for QTL mapping. The four cultivars were chosen for the study because 1) they frequently serve as parental lines for developing new high yield rice cultivars, and 2) they don't share a common ancestor with each other providing a high degree of genetic diversity between the lines. The four cultivars were evaluated in a randomized complete block design (RCBD) with three replications and two planting dates which were 18 May and 6 June in 2017. The cultivars were planted in seven row 3.7x1.5 m plots. The planting depth was 1.3 cm and the spacing between rows was 20.3 cm apart. The germination date was 26 May for the first planting and 15 June for the second planting. Field management was done according to the standard management in Arkansas. At the harvesting season, 10 plants from each plot were randomly collected from the middle part of each plot excluding the edges of the plot. The plants were harvested for evaluation of 14 agronomic traits (Table 1 or 2). The number of filled seeds/plant were calculated by taking the sum of the number of seeds/panicle counted for each plant. The number of spikelets per plant (sp/pl) were calculated by taking the sum of the number of spikelets counted on each panicle from each plant. Seed weigh/plant was calculated by taking the sum weight of all the filled seed produced from a single plant. Panicle length (cm) was measured by measuring each panicle from the base of the rachis to the tip of the top panicle branch and calculating the average

length for each plant. The number of primary panicle branches/panicle were calculated by counting the number of branches growing from the main rachis from each panicle and calculating the average for each plant. Number of blank seed/panicle (bsp/pan) was calculated by counting the number of blank spikelets on each panicle and calculating the average for each plant. Number of seeds/panicle were measured by counting the number of filled seeds per panicle and taking the average per panicle for each plant. Number of spikelets/panicle were calculated by taking the sum of filled seeds and blank spikelets counted for each panicle and calculating the average per panicle for each plant. Seed weight/panicle was calculated by taking the average seed weight per panicle for each plant. One hundred seed weight/panicle was calculated for each panicle using a formula and calculating the average weight per panicle for each plant. The panicles were dried in a grain drier prior to hand threshing for data collection. The plots in the second planting date were harvested to obtain yield/plot for each cultivar. The seed were dried to 12% moisture and weighed in grams. The results from the parental study showed that LaGrue had the highest overall yield and highest seed count among the cultivars due to higher number of primary panicle branches/panicle (Tables 1 and 2). LaGrue had a significantly higher number of filled seeds/plant and seed weight/panicle than Mars and Lemont, and a significantly higher number of filled seeds and spikelets/panicle compared to Lemont (Table 1). In contrast, Lemont had a significantly lower number of seed/panicle, number of spikelets /panicle and number of primary branches/panicle but has a longer panicle length then the other three cultivars. Lemont had significantly higher 100-seed weight/panicle and 1000-seed weight/plant than LaGrue and Mars, but significantly lower seed weight/panicle compared to LaGrue and Bengal. Despite having a significantly longer panicle than other cultivars, it did not help with the yield potential of Lemont (Tables 1 and 2). Based on the results, Lemont and LaGrue were selected for the bi-parental study.

Bi-Parental Population Development

A bi-parental population resulting a cross between LaGrue and Lemont was initiated in the summer 2016. The F1 plants were grown in the spring 2017 in a greenhouse and true F1 plants from selfed plants were identified by means of the molecular study using simple sequence repeat (SSR) markers at the RREC molecular genetics lab. The F2 seed, from each F1 plant, were harvested in the fall 2017 and 322 F2 plants were grown in the greenhouse in the spring 2018 to obtain F2:3 seeds. Meanwhile, the leaf tissue of F2 plants in the greenhouse was sampled for genotypic analysis.

Phenotypic Evaluation of F2:3 Families

In the summer of 2018, 322 F2:3 families derived from the LaGrue × Lemont F2 population were planted in panicle rows at two locations; RREC (34°28'30.5"N 91°25'07.5"W) and the University of Arkansas System Division of Agriculture's Pine Tree Research Station (PTRS) near Colt, Arkansas (35°07'27.4"N 90°55'51.4"W). The two locations were chosen because they both have different soil types (RREC - Crowley silt loam and PTRS - Calhoun silt loam) and are located in two major rice-growing regions in the state of Arkansas which have differing environmental conditions, these environments have been utilized for more than 50 years, The families were planted in a randomized complete block design (RCBD) with three replications for each family. The lines were planted at the PTRS on 10 July and RREC on 11 July. Each replication was planted separately in its own block with ten seeds planted for each line. The F2:3 families were evaluated in the field for plant height (PH hereafter) and 50% heading date (HD hereafter). Plant Height was measured from at least two plants in each row and was measured from the base of the plant to the tip of the main flag leaf to measure the max height of each line when the flag leaf is fully out. Two panicles from each row were sampled to evaluate flag leaf length (FLL hereafter), flag leaf width (FLW hereafter), number of primary panicle branches (PBN hereafter), number of secondary panicle branches (SBN hereafter), and panicle length (PL hereafter). The stand counts at both locations were very low which reduced the amount of panicles and trait measurements collected from the field.

Genotypic Analysis

The LaGrue x Lemont bi-parental F2 population with 322 plants was genotyped using single nucleotide polymorphism (SNP) markers. Leaf tissue from each F2 plant were freeze dried and sent to Eurofins Scientific Inc. to be genotyped using an Infinium 7K Rice SNP chip. About 832 SNP markers were found to be polymorphic in the two parents of the population distributed along the 12 chromosomes of rice

Statistical Analysis

Yield traits for the parental yield study were analyzed using JMP Pro 14 software (SAS Institute Inc., Cary, NC). ANOVA analysis followed by a Student's T-test was carried out to compare yield traits between each cultivar. The traits were measured by calculating the average for each plant. One hundred seed weight/panicle and 1000 seed weight/plant were calculated using the formulas below:

1000 seed weight/plant: $\left(\frac{seed\frac{weight}{plant}}{number\ of\ filled\frac{seeds}{plant}}\right)x1000$

The F2:3 ANOVA and MANOVA analysis on the population was analyzed using PROC GLM in SAS Pro 9.4 to evaluate genotypic and environmental effects on the traits and correlations between traits. The genotype, location, and genotype x location were treated as main effects with Replication (Location) treated as random effects. Broad Sense Heritability was calculated using the formula below:

Broad Sense Heritability: $H^2=\left(\frac{\sigma^2 G}{\sigma^2 P}\right)x100 = ((\sigma^2 G/\left(\sigma^2 G + \left(\frac{\sigma^2 GE}{L}\right) + \left(\frac{\sigma^2 E}{bL}\right)\right)x100$

Where σ^2G: genotypic variance; σ^2P: phenotypic variance; σ^2GE: genotypic x environment; σ^2E: variance associated with error; L: number of locations or environments; b: number of replications or blocks. The σ^2G, σ^2GE, and σ^2E were obtained using the formulas below:

$$\sigma^2G=(MSG-MSGE)/bL$$

$$\sigma^2GE=(MSGE-MSE)/b$$

$$\sigma^2E=MSE$$

where MSG is mean square genotype, MSGE is mean square genotype x location, and MSE is mean square error. The mean square estimates were taken from the ANOVA table in SAS.

QTL Mapping and Candidate Gene Identification

QTL mapping was done using ICI mapping software (Meng et al., 2015). The markers were ordered onto a linkage map using kosambi function. Markers were grouped using a LOD threshold of 4.0 and were ordered on the chromosome using the input function where marker order is known from a physical map. Rippling was done using the sum of adjacent LOD scores function (SALOD). QTL mapping was performed using the Inclusive Composite Interval Mapping of additive and dominant QTL function. A minimal LOD score of 2.5 was used for QTL detection and QTL with a LOD score of 3.0 or higher were declared major. The rice genome database Oryzabase was used to search for potential candidate genes previously mapped within major QTL regions detected (Kurata & Yamazaki, 2006). The positive parental allele for each major QTL was done using simple t-test in JMP Pro 14.

RESULTS

Phenotypic Analysis of LaGrue x Lemont F2:3 Population

The phenotypic variations of seven selected traits were observed among the 322 $F_{2:3}$ lines for QTL analysis. The results revealed that there was near normal distribution on the F2:3 population for each evaluated trait (Fig 1). The ANOVA showed that "Genotype (G)" had a significant effect on the traits PH and HD; "Environment" had a large influence on PH, HD, and PL; and "G×E interaction" had a large effect on HD. Despite being slightly none significant, the results implied there was G effect on PL (p-value 0.0504) (Table 4). Further analysis showed that PH had high broad sense heritability for the trait with 0.7, indicating that the PH was highly heritable (Table 4, Fig.1). The results showed that the SBN (CV=22.7) and HD (CV=6) had the highest and lowest coefficient of variation values, respectively, indicating the largest variation existed in these two traits compared to the other traits measured from the population (Table 4). MANOVA analysis found strong significant correlations between FLL, PL, PBN, and SBN (Table 5). The strongest correlations were found between SBN with PBN (0.63) and PL (0.61). Flag leaf length was strongly correlated with PL, PBN and SPN. Panicle length was also strongly correlated with PBN and SPN. These results show there may be favorable loci in the population that are involved in both panicle development and flag leaf development. It is noteworthy that no negative correlation between the measured traits was found.

QTL Detected for Yield Traits in $F_{2:3}$ population

Flag leaf length and width

To conduct the QTL analysis, the genotypic analysis of 7000 SNP markers were ordered onto a linkage map using kosambi function. A total of 24 QTLs, including 13 major QTLs (LOD>3.0) and 9 minor QTLs, for seven traits were detected in both LaGrue and Lemont and were distributed on 5 chromosomes of 1, 2, 7, 8, and 9. Of 24 detected QTLs, 11 that were found in in LaGrue and the 13 QTLs in Lemont (Table 6). Five different QTLs positioned in two similar genomic regions, *qPH1-3* associated with the PH trait positioned the same genomic region as *qSBN1-2* at chr.1, and *qFLL*8 associated with the FLL trait share the same genomic position with *qPL8-2* associated with *PH t* and *qHD8* associated with HD (Table 6). Three major and one minor QTL were detected for PH trait on chr. 1 and 8 with three QTLs on chr.1 (Table 6). Two QTLs, *qPH1-2* and *qPH1-3,* were co-localized in the same chromosomal position for both Stuttgart and Pine Tree locations with both having very high LOD values of

17.38 and 54.38, respectively (Fig. 2 and 3), and together explained 87% of phenotypic variation. This shows that there might be a major gene that controls plant height in the region. All the QTLs except for the minor QTL, *qPH1-1,* that increased plant height originated from LaGrue. Five QTLs including two major and three minor QTLs for HD trait were detected on chr. 1, 2, 7, and 8 each with one QTL and two QTLs on chr. 7 (Table 6, Fig.s 2 and 3). Two major QTLs, *qHD1* and *qHD8,* explained about 11.75% and 7.23% of phenotypic variation, respectively. Furthermore, all these QTLs were linked to the Lemont allele which delayed heading date. Seven QTLs including five major and two minor QTLs for PL were detected on chr. 1, 7, 9 each with one QTL and chr. 2 and 8 each with two QTLs (Table 6, Fig.s 2 and 3). Two QTLs on chr. 8 *qPL8-1* and *qPL8*-2 positioned near each other on chr. 8 explained 18.5% of phenotypic variation in the population. LaGrue was the major contributor to increased panicle length in *qPL1, qPL2-1,* and *qPL2-2* while Lemont was the major contributor in *qPL8-1,* and *qPL8-2* (Table 6, Fig.s 2 and 3). One major QTL for number of primary panicle branches *qPBN1* was detected on chr. 1 where LaGrue was the positive parental allele (Fig. 3). Three QTLs including one major and two minor QTLs for SBN trait were detected on chr. 1 and 9 with two QTLs on chr. 1 (Table 6). The major QTL, *qSBN1-1*, explained about 16.3% of phenotypic variation and had a positive allele from LaGrue that increased the number of secondary branches per panicle. The QTL *qSBN1-1* and *qSBN1-2* were detected near each other on chr. 1 (Table 6, Fig.s 2 and 3). Three QTLs for the FLL trait including 1 major and 2 minor QTLs were detected. The major QTL qFLL8 located on chr.8 explained about 8% of the phenotypic variation and had positive allele with Lemont One major QTL, *qFLW2,* for FLW was detected on chr. 2 explaining 9.21% of phenotypic variation in the population (Table 6, Fig.s 2 and 3).

Candidate Gene Analysis

Using the online rice database Oryzabase, a total of 9 candidate genes were found with two genes on chr.1 and seven genes on chr.8 controlling plant height, panicle development, and flag leaf size (Table 7). The genes on chr.1 are semi-dwarf 1 (*sd-1*) and *DCL3a.* (Table 7). A previous study reports the importance of this location on plant height since the semi-dwarf *sd-1* locus encodes a defective 20-oxidase GA biosynthesis enzyme involved in the synthesis of gibberellin located in the two QTL *qPH1-3* and *qPH1-4* (Sasaki et al. 2002). The *DCL3a* gene is a Dicer-like 3 homolog located near *qPBN1* that produces a 24-nt small interfering RNA (Wei et al., 2014). The gene was found to control plant height as well as panicle development.

The genes found on chr.8 are *UBP1-5*, *UBP1-8*, Wide and Thick Grain 1 (*WTG1*), *OsSPL16*, *OsSPL14*, *OsCOL15*, and *OsMADS7* (Table 7). *UBP1-5* and *UBP1-8* are ubiquitin carboxyl-terminal hydrolase genes that were found to be significantly upregulated during panicle development (Ke et al. 2018). *WTG1* is a gene that encodes an otubain-like protease with deubiquitination activity (Huang et al. 2017). The gene was found to control panicle development affecting the number of primary and secondary branches and also number of seed per panicle. The gene was also found to control *OsSPL14* through degradation of K63-linked ubiquitin chains of the protein (Wang et al. 2017) The gene *OsSPL14,* otherwise known as Wealthy Farmer's Panicle, encodes a SQUAMOSA PROMOTER BINDING PROTEIN-LIKE 14 protein and is located in the QTL *qPL8-1* (Miura et al., 2010). The gene was found to control number of primary and secondary branches per panicle, tiller number, flag leaf size, plant height, grain yield, number of seeds per panicle, 1000-grain weight, and lodging resistance. *OsSPL16* is a squamosa promoter-binding protein transcription factor associated with grain size and 1000 grain weight (Wang et al. 2012, 2015). The gene was also found to control another gene involved in grain size *GW7* through binding to the promoter and inhibition gene expression (Wang et al. 2015). *OsCOL15* is a CONSTANS-like transcription factor located in the QTL *qHD8* that regulates flowering time by influencing flowering genes and acts as a floral inhibitor (Wu et al. 2018). *OsMADS7* (or otherwise known as *OsMADS45*) is a MADS-box class-E class gene which controls flowering as well as plant height, tiller number, number of spikelets per panicle, and grain yield (Cui et al. 2013; Wang et al., 2013). The gene was found to influence flowering genes *RFT1, Hd3a, OsMADS14, and OsMADS18* in controlling flowering time.

Discussion

Increasing rice seed yield is the outmost goal in rice breeding program. a high yielding rice cultivar is developed from parental lines with favorable agronomic characteristics such as LaGrue and Lemont that have been used frequently for developing high yield cultivars in the U.S. Moreover, identification of QTLs controlling favorable agronomic characteristics in LaGrue and Lemont would be valuable for the breeding of high-yielding rice cultivsrs. Lemont and LaGrue were evaluated on several agronomic traits associated with yield. Many QTLs associated with seed yield production have been identified and applied in rice breeding programs (Miura et al., 2011). Plant height is one important trait since tall rice plants tend to lodge easier that short ones. The results showed *qPH1-2* and *qPH1-3*, were adjacent to each other on chr. 1 and explained a significant phenotypic variation

in the population. The trait was highly heritable in the population having a broad sense heritability of 0.70. Our result is supported by previous efforts by IRRI (1967) that integrated a recessive semi-dwarf gene (*sd-1*), which was found earlier in China, as well as genomic detection of *sd-1* (Monna et al, 2001; Sasaki et al. 2002) that is co-localized by the detected QTLs. The gene causes a semi-dwarf height in rice without affecting grain yield. The semi-dwarf height also decreases the chance of lodging in rice increasing the potential harvestable yield of rice cultivars. The gene was very important in Asia in the development of high-yielding rice cultivars with reduced susceptibility to lodging (Sasaki et al., 2002). The gene *sd-1* gene came from Lemont since LaGrue does not have the gene *sd-1*.

Panicle traits, including panicle length, primary branch number, secondary branch number, and spikelet number, are considered as some of the most important components in seeds yield production (Cheng et al. 2007; Peng et al. 2014; Shang et al. 2020). Increasing panicle size has a positive correlation with other panicle traits as well as FLL and HD, and as a result, it can be assumed that increasing any of these panicle characteristics such as panicle size can improve seed yield production. Our assumption is supported by a previous study by Shang et al., (2020) Also the QTL analysis showed that those QTLs with higher phenotypic variation originated from LaGrue which had the longer panicle. On chr. 8, major QTLs for PL and FLL were co-localized in a 3.2Mbp region, so it can be assumed the positive correlation between PL and FLL resulted in this relationship. All the major QTLs which increased FLL and PL on chr. 8 came from Lemont. Five potential candidate genes for the traits *UBP1-5*, *UBP1-8*, Wide and Thick Grain 1 (*WTG1*), *OsSPL16* and *OsSPL14* were found in these QTL regions. The genes *UBP1-5*, *UBP1-8* were found to be upregulated during panicle development (Ke et al. 2018). Wide and Thick Grain 1 (*WTG1*) is a gene that affect grain size, panicle architecture, 1000 seed weight, and flag leaf width (Huang et al. 2017). This gene was found to interact with another gene in the region *OsSPL14* or otherwise known as Wealthy Farmer's Panicle (Wang et al. 2017) *OsSPL14* induces an ideal plant architecture such as increased number of primary and secondary branches, increased number of seeds per panicle, increase in length of flag leaf length and reduced lodging. Reduced gene expression of *WTG1* was found to increase the expression of *OsSPL14* giving an ideal plant type in rice (Huang et al. 2017). *OsSPL16* controls grain size, panicle branching, and 1000 grain weight and may control grain size through regulation of *gw7* (Wang et al. 2012, 2015). Because there is a positive correlation, analysis showed that FLL and PL, PNB, and SNB, could be genes such as *OsSPL14* and *WTG1* and therefore, could be potential targets for molecular breeding. One major QTL for FLW was found on chr. 2 that came from Lemont that increased leaf width.

Gramene search found previous reports that found a QTL that overlapped the panicle length QTL *qPL-1* on chr. 1 (Thomson et al. 2003; Hittalmani et al. 2002, 2003; Septiningsih et al. 2003). Two reports also found QTL, *qPL2-2,* and *qPL7,* that overlapped the QTL regions for *qPL2-1, qPL2-2,* and *qPL7-1* (Mei et al. 2003, 2005).

Five QTL for heading date were detected on chr. 1,2,7, and 8 with one major QTL *qHD1* explaining 11.76% of phenotypic variation in the population. All the major QTL for heading date came from Lemont which increased days to heading. Two candidate genes for heading date were detected in *qHD8*; *OsCOL15* and *OsMADS7*. *OsCOL15* is a floral inhibitor that delays the days to heading in rice (Wu et al. 2018). The gene influences heading date by upregulating the flowering gene *Ghd7* and inhibiting *RID1* which in turn influences other genes such as *Ehd1, Hd3a, and RFT1*. *OsMADS7* is another flowering gene that participates in regulation of floral development (Cui et al. 2010). The gene has been found to control flowering as well as plant height, panicle length, tiller number, number of spikelets per panicle, and grain yield (Wang et al. 2013) The gene was found to control four other genes, *RFT1, Hd3a, OsMADS14,* and *OsMADS18* which may contribute to flowering and vegetative growth (Wang et al. 2013) Whereas the gene is found to control panicle length and number of spikelets per panicle, it could be considered a candidate gene for yield traits as it is found in the same regions as *qPL8-2* and *qFLL8-2*. Reports from other studies found QTL for heading date that overlapped with the QTL region for *qHD1* (Li et al. 2003; Hittalmani et al. 2003; Thomson et al. 2003). Surprisingly, the heritability for heading date was low with a broad-sense heritability of 0.21.

Three QTLs for SBN were found on chr. 1 and 9. Two QTLs, *qSBN1-1* and *qSBN1-2*, were found close together on chr. 1 with *qSBN1-1* having the highest LOD and was responsible for 16.3% of phenotypic variation in the population. One major QTL for PBN was found on chr. 1. The major QTL for primary and secondary branch number *qPBN1* and *qSBN1-2,* were found to come from LaGrue which increased the number of panicle branches. This was expected considering LaGrue produces a significantly higher number of seed than Lemont. One candidate gene *DCL3a* was found near *qPBN1* that was found to control both PBN and SBN (Wei et al. 2014)

CONCLUSION

Improving grain yield in rice is one of the important goals in rice breeding programs. Overall grain yield in rice is dependent on several yield components such as plant height, number of seeds per panicle, and 1000 seed

311 weight (Xing et al., 2010). The detection of major QTL for yield components can be beneficial for breeding of high-
312 yielding rice varieties. Results from this study showed major QTLs for PH, FLL, PL, PNB, SNB traits were found.
313 The results from this study can be used by breeders for selecting superior lines via marker assisted selection.

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564 **Table1:** Comparisons of yield traits among four cultivars.

Trait	LaGrue	Lemont	Bengal	Mars
No. filled seeds/plant	1812.9[a]	1277.4[b]	1428.7[ab]	1333.1[b]
No. spikelets/plant	2078.8[a]	1405.2[b]	1874.4[ab]	1735.3[ab]
No. blank spikelets/plant	264.3[b]	127.7[c]	445.3[a]	402.6[a]
Seed weight/ plant, g	43.4[a]	34.2[ab]	37.5[ab]	31.2[b]
1000 seed weight/Plant	24.0[b]	26.5[a]	26.1[a]	23.3[b]
Panicle Length, cm	19.9[b]	20.8[a]	20.1[ab]	20.1[ab]
No. primary panicle branches/panicle	11.9[a]	10.8[b]	11.1[b]	11.3[b]
No. filled seeds/panicle	121.7[a]	88.7[b]	113.7[a]	113.7[a]
# spikelets/panicle	139.1[a]	98.0[b]	148.3[a]	147.4[a]
No. blank spikelets/panicle	17.4[b]	9.2[c]	34.7[a]	36.3[a]
100-seed weight/panicle, g	2.4[b]	2.6[a]	2.6[a]	2.3[c]
Seed weight/panicle, g	2.9[a]	2.4[b]	3.0[a]	2.6[b]
No. tillers/Plant	14.0[ab]	14.6[a]	11.4[b]	12.3[ab]
No. panicles/Plant	13.8[ab]	14.5[a]	11.1[b]	12.0[ab]

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Table 2: Evaluation of plot yield between rice cultivars

Cultivar	Average yield per plot (g)	Yield difference compared to LaGrue	Percentage yield increase of LaGrue (%)
LaGrue	2004.47	0	0
Bengal	1883.37	-121.1	6
Lemont	1693.17	-311.3	15.5
Mars	1572.87	-431.6	21.5

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603 **Table 3:** Yield Analysis of Parental Controls and descriptive statistics of the $F_{2:3}$ Population

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Trait†	LaGrue Mean‡	Lemont Mean	Mean (cm)	Range (cm)	Standard Dev. (SD)	Standard Err. (SE)	CV
PH (cm)	101^{a}	90^{b}	99.1	66.5-136.5	11.8	0.33	11.8
HD (day)	79.8^{a}	82^{a}	79.4	69-94	4.8	0.14	6
FLL(cm)	26.3^{a}	28.3^{a}	27.5	16.4-46.8	4.4	0.13	16.2
FLW(cm)	1.2^{a}	1.3^{a}	1.2	0.6-1.9	0.2	0.0059	16.9
PL(cm)	23^{a}	23.9^{a}	23.3	16.8-31.8	2.4	0.068	10.1
PBN	23.2^{a}	23.3^{a}	23.1	12.0-34.0	3.5	0.1	14.9
SBN	36.6^{a}	34^{a}	37.7	14-68.5	8.6	0.25	22.7

605 † Traits; PH, plant height; HD, Days of heading; FLL, Flag leaf length; Flag leaf width; PL, Panicle length; PBN,
606 Number of primary branches; SBN, Number of secondary branches
607 ‡ Significance of 0.05 given by abc subscript
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Table 4: ANOVA analysis of yield traits in $F_{2:3}$ population

Trait†	Genotype‡	Location§	Genotype x Location	Mean Square Err.	Heritability
PH (cm)	209.82** <.0001	19829* 0.0084	62.91 0.4254	61.65	0.7
HD (day)	17.87** 0.0001	5196.40* 0.0087	14.24* 0.0436	11.62	0.21
FLL(cm)	20.88 0.2616	3.49 0.7404	19.063 0.5834	19.62	0.08
FLW(cm)	0.038 0.1153	1.39 0.3199	0.030 0.8263	0.033	0.19
PL(cm)	4.95 0.0504	688.65* 0.0007	4.14 0.5429	4.21	0.17
PBN	11.65 0.3092	227.44 0.2513	9.67 0.8612	11.1	0.27
SBN	78.38 0.0516	545.34 0.2764	64.58 0.6002	66.81	0.17

† Traits; PH, plant height; HD, Days of heading; FLL, Flag leaf length; Flag leaf width; PL, Panicle length; PBN, Number of primary branches; SBN, Number of secondary branches

‡ Effects with P-values less than 0.01 given **

§ Effects with P-values less than .0001 given *

Table 5: Correlations between yield traits in F2:3 population

Trait†	Plant Height‡	Days to heading	Flag Leaf Length	Flag Leaf Width	Panicle Length	Primary Branch Number	Secondary Branch Number
PH (cm)	1	0.052489 0.1925	0.191061 <.0001*	0.167098 <.0001*	0.105132 0.0089	0.121957 0.0024	0.165395 <.0001*
HD (day)	0.052489 0.1925	1	0.1798 <.0001*	0.018196 0.6517	0.270397 <.0001*	0.15137 0.0002	0.241675 <.0001*
FLL(cm)	0.191061 <.0001*	0.1798 <.0001*	1	0.189338 <.0001	0.574084 <.0001*	0.41541 <.0001*	0.433789 <.0001*
FLW(cm)	0.167098 <.0001*	0.018196 0.6517	0.189338 <.0001*	1	0.029408 0.4655	0.223711 <.0001*	0.111571 0.0055
PL(cm)	0.105132 0.0089	0.270397 <.0001*	0.574084 <.0001	0.029408 0.4655	1	0.475573 <.0001*	0.610198 <.0001*
PBN	0.121957 0.0024	0.15137 0.0002	0.41541 <.0001*	0.223711 <.0001*	0.475573 <.0001	1	0.635593 <.0001*
SBN	0.165395 <.0002	0.241675 <.0001*	0.433789 <.0001*	0.111571 0.0055	0.610198 <.0001*	0.635593 <.0001*	1

† Traits; PH, plant height; HD, Days of heading; FLL, Flag leaf length; Flag leaf width; PL, Panicle length; PBN, Number of primary branches; SBN, Number of secondary branches

‡ Effects with P-values less than 0.01 given *

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691 **Table 6:** List of QTL detected and parental origin of positive allele for major QTL
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Trait	QTL	Positive Parental Allele	Location	Left Marker	Right Marker	BP Position	LOD	PVE(%)	Add	Dom
FLL	*qFLL2-1*		ST	c2p19270352	id2007542	19,270,353-19,294,608	2.70	5.81	-0.71	-0.80
	qFLL2-2		ST	SNP-2.28645110.	2369745	28,650,980-31,203,132	2.57	5.74	0.34	1.18
	qFLL8	Lemont	ST	SNP-8.26142013.	9030959	26,144,728-27,300,242	3.13	8.03	-1.11	0.51
	qFLW2	Lemont	ST	2051794	SNP-2.21778435.	21,329,057-21,784,305	4.04	9.21	-0.05	-0.03
HD	*qHD1*	Lemont	PT	id1025292	1277001	39,799,820-40,032,941	9.44	11.76	-1.43	-0.36
	qHD2		PT	2078559	id2010564	22,089,558-24,693,023	2.67	3.27	-0.83	0.07
	qHD7-1		PT	7094244	rd7002048	5,185,191-6,855,960	2.54	3.55	-0.31	1.06
	qHD7-2		ST	SNP-7.21232810.	id7004163	21,233,804-23,427,756	2.73	3.45	-1.88	-2.63
	qHD8	Lemont	PT	SNP-8.26142013.	9030959	26,144,728-27,300,242	5.51	7.23	-1.10	-0.32
PL	*qPL1*	LaGrue	ST	SNP-1.37415410.	1212517	37,416,454-37,692,801	4.83	11.15	0.64	0.29
	qPL2-1	LaGrue	ST	id2004711	SNP-2.11601520.	9,880,575-11,601,525	3.98	9.90	0.46	-0.44
	qPL2-2	LaGrue	PT	SNP-2.11601520.	c2p17996374	11,601,525-17,996,375	3.10	5.09	0.46	-0.06
	qPL7-1		PT	rd7002219	id7004930	24,113,175-25,945,760	2.96	5.10	-0.48	-0.14
	qPL8-1	Lemont	ST	id8006881	8980373	24,803,160-25,658,584	4.42	10.12	-0.55	-0.20
	qPL8-2	Lemont	PT	SNP-8.26142013.	9030959	26,144,728-27,300,242	5.14	8.46	-0.57	-0.24
	qPL9		ST	rd9002652	9563291	10,798,265-12,154,616	2.82	6.21	-0.26	0.46
PBN	*qPBN1*	LaGrue	ST	1259171	SNP-1.39395295.	39,342,234-39,396,339	3.36	8.14	0.71	0.41
PH	*qPH1-1*		ST	222467	SNP-1.7150499.	7,116,232-7,151,500	2.85	4.68	-0.54	-3.09
	qPH1-2	LaGrue	ST	SNP-1.38422515.	SNP-1.38536811.	38,423,559-38,537,855	17.38	32.86	6.38	2.27
	qPH1-3	LaGrue	PT	1226391	rd1000365	38,258,929-38,361,942	54.39	55.11	9.90	-0.01
	qPH8	LaGrue	PT	SNP-8.26090329.	SNP-8.26142013.	26,093,044-26,144,728	3.65	2.38	2.01	0.29
SBN	*qSBN1-1*	LaGrue	ST	SNP-1.38536811.	1237300	38,537,855-38,652,270	7.58	16.27	3.14	0.91
	qSBN1-2		PT	1226391	rd1000365	38,258,929-38,361,942	2.83	4.37	1.77	-0.35
	qSBN9		PT	rd9002719	SNP-9.17707021.	17,416,860-17,708,023	2.99	4.74	1.87	-0.07

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694 † Traits; PH, plant height; HD, Days of heading; FLL, Flag leaf length; Flag leaf width; PL, Panicle length; PBN,
695 Number of primary branches; SBN, Number of secondary branches

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699 **Table 7:** List of candidate genes for yield traits

Gene Id	Gene	Chromosomal Position (bp)	Trait	Description
LOC_Os01g66100	sd-1	Chr 1: 38382382 - 38385504	PH	semi dwarf 1 gene
LOC_Os01g68120	DCL3A	Chr1: 39605717 - 39595681	PBN	Endoribonuclease Dicer homolog 3a
LOC_Os08g41580, Os08g0527600	UBP1-5	Chr 8: 26268141-26263393	PBN, SBN	ubiquitin carboxyl-terminal hydrolase
LOC_Os08g41630, Os08g0528100	UBP1-8	Chr 8: 26299397 - 26287372	PBN, SBN	ubiquitin carboxyl-terminal hydrolase family protein
LOC_Os08g42540	OTUB1, WTG1	Chr 8: 26887363 - 26882955	PFL	ubiquitin thioesterase otubain-like
LOC_Os08g41940	GW8,OsSPL16	Chr 8: 26501167 - 26506218	HD	SBP-box gene family member
LOC_Os08g39890	Wealthy farmers panicle, IPA 1,WFP,OsSPL14	Chr 8: 25278696-25274449	PFL	SBP-box gene family
LOC_Os08g42440	OsCOL15	Chr8: 26797181 - 26792824	HD	CCT/B-box zinc finger protein
LOC_Os08g41950	OsMADS7,S45	Chr 8: 26507753 - 26512261	HD	MADS-box family gene with MIKCc type-box

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Figures

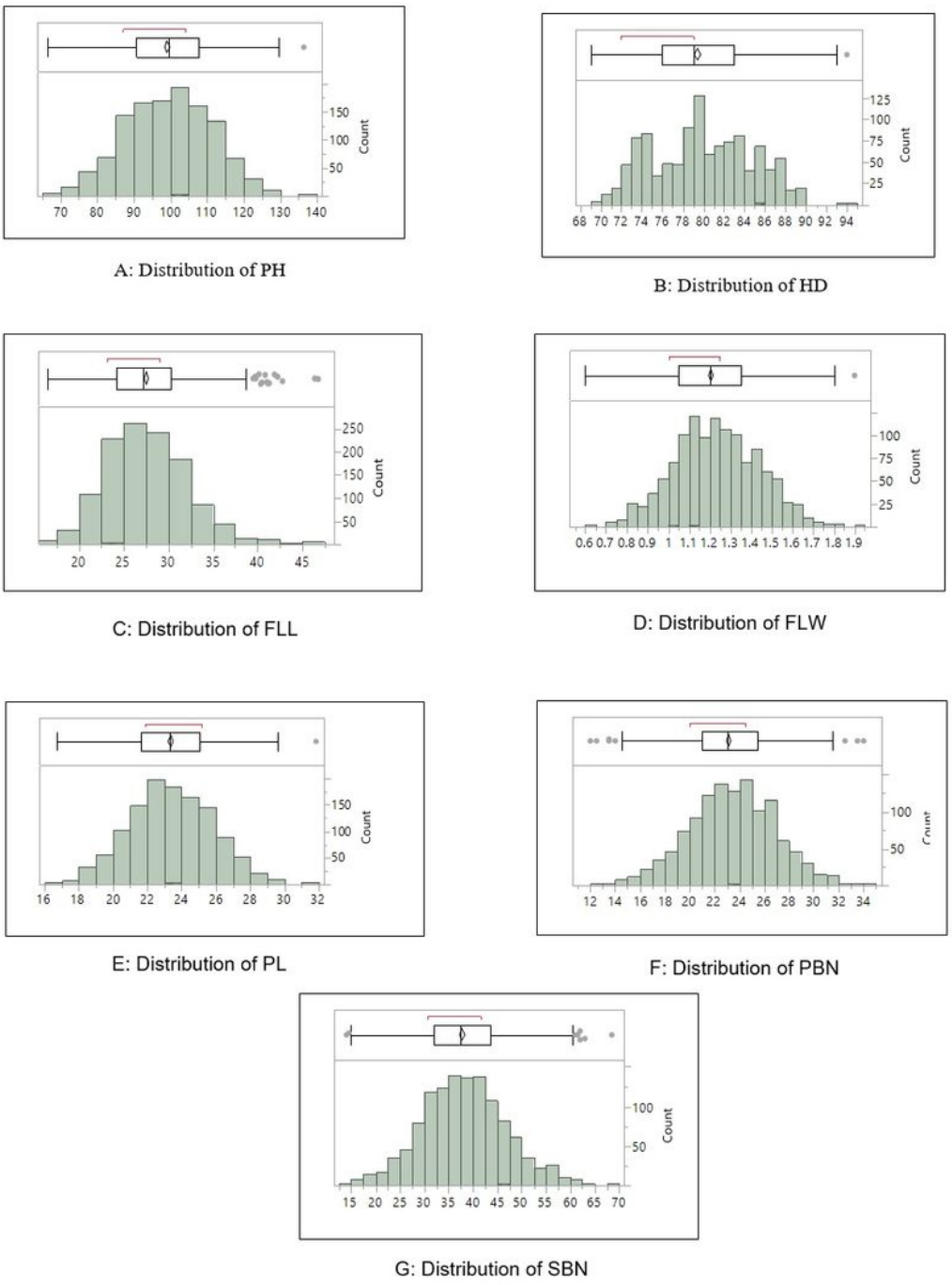

Figure 1

A-G: Distribution of Yield Traits in F2:3 population † Traits; PH, plant height; HD, Days of heading; FLL, Flag leaf length; Flag leaf width; PL, Panicle length; PBN, Number of primary branches; SBN, Number of secondary branches

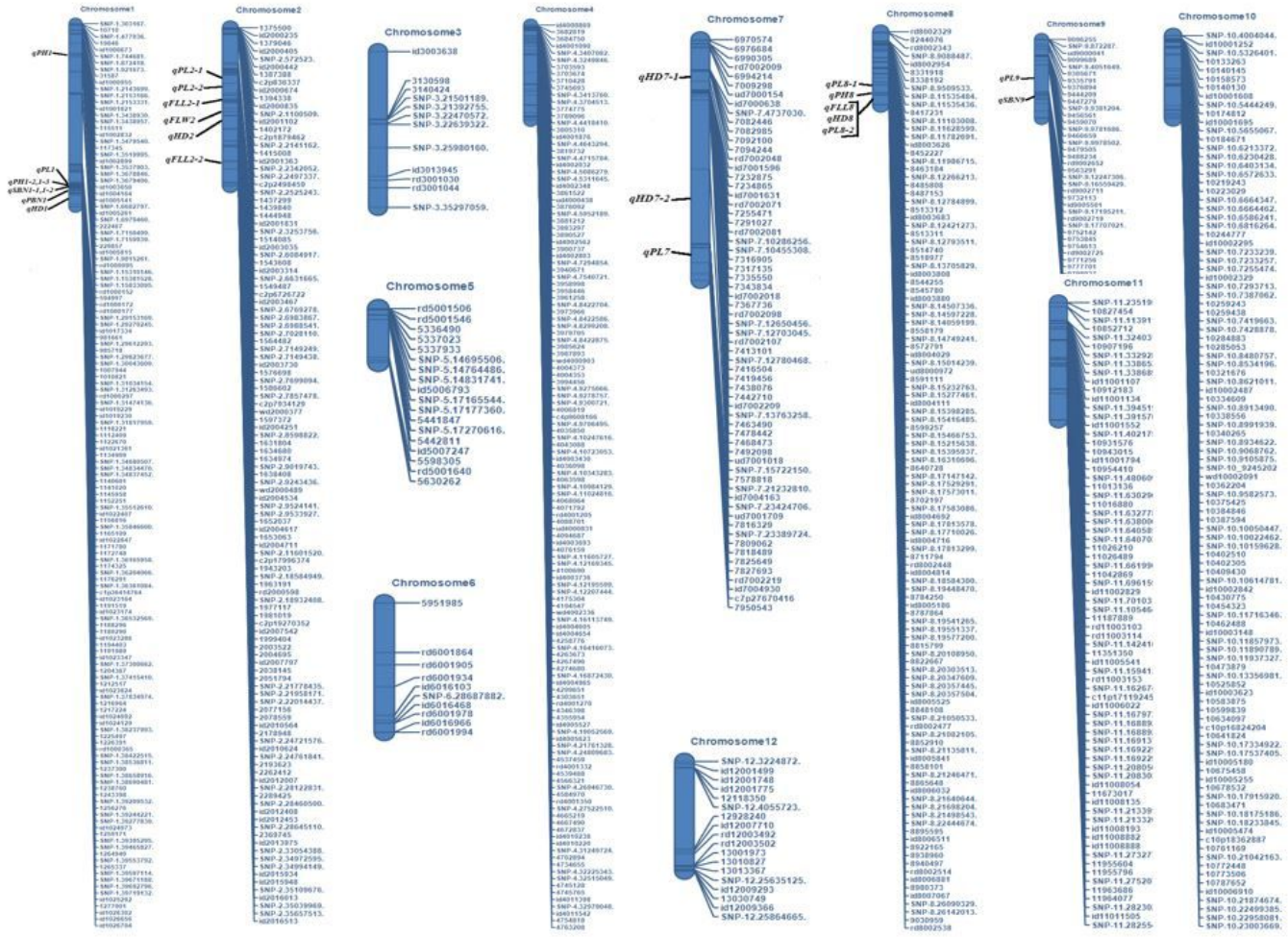

Figure 2

Linkage Map and QTL position in Pine Tree

Image not available with this version

Figure 3

One major QTL for number of primary panicle branches qPBN1 was detected on chr. 1 where LaGrue was the positive parental allele (Fig. 3).