**Genetic Characterization of Germination Traits and Their Relationship to Preharvest Sprouting in Winter and Spring Barley**

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**Executive summary**

This grant supported a single-year project to better understand the genetic control of preharvest sprouting (PHS) and seed dormancy in a winter/facultative double haploid population. This project produced genome-wide Illumina 50K marker data on a population of Cornell winter and facultative breeding lines and characterized these same populations for PHS, germination rate, and germination energy from physiological maturity to 6 months post-harvest. The genetic data will facilitate the identification of superior malting barley varieties and trait characterization in relevant breeding germplasm. The data collected in this study (susceptibility to PHS, germination rate, and germination energy) has increased understanding of winter malting barley seed dormancy and dormancy persistence and will allow for the selection of PHS resistant lines, with quick dormancy break and rapid germination rate gain.

Theis grant has also enhanced knowledge of the genetics of the *SD2* locus in spring barley. Data presented here strongly suggests that at least three functional alleles of *HvMKK3* with different effects on PHS, primary seed dormancy, and germination rate are present in North American malting barley germplasm. These alleles interact with *HvAlaAT1* in different ways and these relationships change over the after-ripening period. The role of *HvGA20ox1* in PHS and seed dormancy is still unclear. High-throughput KASP assays were developed that precisely detect polymorphisms in large effect seed dormancy genes that are not in high LD with 50k chip markers. These results further give hope to the development of high malting quality, PHS resistant barley varieties, especially for the craft brewing market.

**Detailed Report on Objectives, Methodology and Results – AMBA Funded Project**

**Section 1: Winter Barley**

Objective 1: Genetic characterization of a winter barley double haploid population using 50K Illumina sequencing marker data and KASP markers

The winter barley germplasm was developed by crosses to the common parent DH130910 (now cv. Lightning) to parents Flavia, KWS Scala, SY Tepee, and Wintmalt. At the time of crossing in fall 2017, parents KWS Scala, SY Tepee and Flavia were prominent winter barley lines that had good yield, moderate disease resistance, and high malting quality in Cornell regional trials. As of 2021, KWS Scala continues to be the most widely grown winter barley in New York state. Wintmalt was chosen as a superior malt quality donor. The common parent DH130910 was developed by Oregon State University (OSU) and was chosen for its high yield, moderate disease resistance, and facultative growth habit. F1 seed from each cross was sent to OSU for double haploidization and DH plants were returned to Ithaca in summer 2018. Two locations of headrows were planted in the 2019-2020 growing season. Checks in both locations included the parental lines and Charles, a PHS and disease susceptible line in New York. Seed from 2019-2020 was used for yield plots at two locations for the 2020-2021 growing season and additional seed was sent to OSU for further collaborative projects. Two preliminary yield trials were planted for the 2021-2022 growing season. Each location consisted of 435 unique DH lines replicated once at each location. Checks for both locations included the common parent Lightning(DH130910), KWS Scala and Endeavor as a PHS, disease susceptibility and AMBA recommended variety check.

Materials and methods

PHS was measured by harvesting 5 spikes per headrow at physiological maturity (PM), after-ripening for 3 days, and then misting in a greenhouse for 3 days, after which the spikes were assessed for PHS on a 0 to 9 scale. Due to labor constraints brought on by the pandemic in the 2020 year, phenotyping capacity was limited and germination was prioritized over PHS to better meet the objectives of this grant. PHS was phenotyped on a sub-sample of 100 lines from one location. The sub-sample consisted of all facultative types across all four families, parental checks, and Charles. For 2021, Twelve to fifteen additional spikes were sampled from headrows of 444 lines in two locations two days after 50% of the headrow reached PM for use in germination tests. Some lines were omitted due to poor winter survival and low seed quality. Spikes were dried for 48 hours before being hand threshed and frozen at -20 C. Grain was removed from the freezer 24 hours prior to starting the assays and stored at ambient lab temperature and humidity for the duration of the experiment. Germination energy (GE) and germination index (GI) were measured at five time points for 2020: 5 (TP1), 19 (TP2), 47 (TP3), 96 (TP4), and 152 (TP5) days post PM. Germination Energy(GE) and germination index(GI) were measured at eight time points for 2021: 5(TP1), 12(TP1.5), 19 (TP2), 33(TP2.5), 47(TP3), 68 (TP3.5), 96 (TP4) and 152(TP5) days post PM. Germination tests followed the American Society of Brewing Chemists (ASBC) method for GE with two modifications. The first modification was the use of 30 kernels instead of 100 kernels. The second modification was an extended germination count from 3 days to 5 days in lieu of counting for 3 days and using H2O2 to break dormancy. In brief, GE was calculated as the percentage germinated kernels after three days and for five days. Germination index was calculated as:

*3 Day GI =10 (N24+N48 +N72)/ (N24+2N48 +3N72)*

*5 Day GI =10 (N24+N48 +N72 +N96+N120)/ (N24+2N48 +3N72+4N96 +5N120)*

where N24, N48, N72, N96 and N120 were the number of germinated kernels at 24, 48, 72, 96 and 120 hours after the start of the assay. For analysis GI was scaled by GE as GIscale = GI\*GE to account for low germination at TP1 and TP2.  For TP1 in 2020, a subset of the lines (223) was phenotyped compared to the remaining timepoints (444). The TP1 subsample included sampling of all checks (30), lines tested for PHS (100), and a random sample from each family for the remaining lines.

All lines were genotyped with the 50k Illumina Infinium iSelect SNP array at the USDA Small Grains Genotyping Lab in Fargo, ND. After filtering poor quality markers, minor allele frequency (MAF) below 0.05, and monomorphic sites, 15,467 polymorphic markers remained and were used for genome-wide association (GWA). After conducting linkage disequilibrium (LD) pruning to reduce high LD blocks that exist in double haploid populations, we retained 8,384 markers for analysis. The *GAPIT* R package (Tang et al., 2016) was used for GWA. Multi-locus mixed models (MLMM) were fit for germination traits at each time point and for PHS. MLMM models have fewer false positive associations and use forward and backward step-wise regression compared to the standard mixed linear model.  P-values below the Bonferroni cutoff (p=0.05) of 3.57x10-6 were considered significant. A summary of the GWA results is presented in Table 1. Models were run for all trait/time point combinations, including the 5-day extensions.

Results

*\*In the previous cycle report, we indicated that AlaAT\_L214F KASP marker was not a significant marker in our GWA. We found an error in our genetic matrix where the AlaAT KASP marker was not in correct position. After corrcecting this mistake, our results definifively indicate that AlaAT a major effect loci in dormancy for our winter malting barley population.*

PHS scores were low in both variation and mean. This was not surprising as parents DH130910, SY Tepee, KWS Scala and Flavia have had consistently low PHS scores in variety trials over multiple years. Correlation to TP1 GE values was 0.43. More PHS data needs to be collected in the future to determine the relationship between PHS and germination traits.

Figures 1 and 2 show GE and GI best linear unbiased estimators (BLUEs) for each family across all five timepoints. Dotted lines indicate the checks. All parents had dormant alleles for *HvMKK3*  and *HvGA20ox1*. Flavia and DH130910 had dormant alleles at AlaAT\_L214F. Given the low PHS scores of the parents in variety trials and the presence of dormant alleles of known seed dormancy genes, the observed GE and GI values at early time points were higher than expected. DH130910 exhibited strong primary seed dormancy greater than the parental checks and most experimental lines.  Germination traits in Flavia, Scala and Wintmalt families were normally distributed between values for each parent, suggesting additive effects controlling germination. The SY Tepee family germination trait values were skewed towards values of each parent, suggesting a large role of non-additive effects in controlling germination in this family. GE differentiation was most prevalent in earlier timepoints and by TP4, most lines across all families were non-dormant and achieved germination energy values similar to Charles. Closer analysis of phenotypes separated by AlaAT\_L214F allele suggested that AlaAT\_L214F was contributing to seed dormancy in the population, but AlaAT\_L214F was surprisingly not detected as a significant marker in GWA.

18 unique markers were associated with the measured germination traits. The largest effect locus found for all germination traits was detected by marker JHI-Hv50k-2016-311497, located on chromosome 5H at ~475 Mbp. Other significant markers were located within 2,200,000 bp of JHI-Hv50k-2016-311497, including JHI-Hv50k-2016-311574 and JHI-Hv50k-2016-311960. Marker allele frequencies of JHI-Hv50k-2016-311574 and JHI-Hv50k-2016-311960 differ slightly from JHI-Hv50k-2016-311497 but high LD between the three markers suggests they are detecting the same locus. The LD between JHI-Hv50k-2016-311497 and AlaAT\_L214F gene was low (~0.25) but surprisingly the AlaAT\_L214F marker was not detected in the GWA, despite its known effect in spring populations. Grouping lines by the AlaAt\_L214F allele revealed a clear differentiation in phenotypic traits(Figure 3), which suggests that it should have been detected in a GWA model, particularly at the intermediate timepoints. Further analysis of the marker region is needed to determine why the effects of the AlaAT\_L214F marker are not being detected. Viewing the evidence from the winter dataset in concert with the spring dataset suggests there may be a novel seed dormancy locus in the region. A marker in the same region (JHI-Hv50k-2016-311615) was just below the significance threshold for 5-day GE and GI for the spring barley population. Isoamylase 3 (*HvISA3*, HORVU.MOREX.r2.5HG0404420) is a starch-debranching enzyme located at 475796690-475807295 bp, 93619 bp distal to marker JHI-Hv50k-2016-311615. Isoamylases hydrolyze α-(1,6) glycosidic linkages and debranch amylopectin during grain filling (Gous and Fox, 2017). Shu and Rasmussen (2014) identified a MTA for amylose content highly associated with the contig MLOC\_10776, which includes *HvISA3* (https://ics.hutton.ac.uk/morexGenes/). Starch with higher amylose content is hydrolyzed more slowly by amylolytic enzymes and higher amylose content has been hypothesized to be a contributing factor to grain dormancy (Chu et al., 2014). Although the role of amylose content in seed dormancy has been hypothesized, prior evidence for the role of *HvISA3* is limited. This locus may be useful for PHS resistance but a consistent decrease in GI is not desirable. Negative impacts on starch related malting quality traits like malt extract may also be present.  Another gene of interest in this region is an abscisic acid responsive protein (Liu et al. 2013). Abscisic acid (ABA) is an important regulator of seed dormancy in barley: increases in ABA maintain seed dormancy and decreases in ABA reduce seed dormancy in barley (Gómez-Cadenas et. al 1999). Other potential novel loci include HvVP1 (Viviparous-1) which may be associated with JHI-Hv50k-2016-198312 on chromosome 3H and segregating in the SY Tepee family. HvVP1 is a master transcription factor regulator that controls switching between seed maturation and germination in barley (Abraham et al. 2016).

Going forward, we plan to further investigate the AlaAT1\_L214F locus interaction with JHI-Hv50K-311497 region and understand why AlaAT1\_L214F is not a significant marker trait association. We also will be examining other genes located near significant markers of this study to understand their effects on germination energy and rate. For the 2020-2021 season, we have planted 435 DH lines (+45 checks) in yield plots at two locations. This yield plot level population will be a valuable resource for phenotypes where larger seed quantities are needed for accurate measurement.

Table 1: Marker-trait association summary for germination trait genome-wide association. The “Genes of interest” column indicates nearby (+/- 1000000 base pairs) genes that have been implicated in seed germination or dormancy in the literature. Empty cells indicate no previously reported genes in the marker region

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| --- | --- | --- | --- | --- | --- | --- |
| **Trait\*** | **Marker** | **Chr** | **Position** | **MAF\*\*** | **p values\*\*\*** | **Genes of interest** |
| TP2-GI\_5D, TP2-GI | JHI-Hv50k-2016-73697 | 2H | 24211311 | 0.357 | 3.39x10-7 | Pseudo-response regulator HORVU.MOREX.r2.2HG0088670 |
| TP2-GE | JHI-Hv50k-2016-73780 | 2H | 24228737 | 0.353 | 1.17x10-6 | Arogenate dehydratase-HORVU.MOREX.r2.2HG0088340 |
| TP5-GE,TP4-GE\_5D,TP4-GE | JHI-Hv50k-2016-106350 | 2H | 577412613 | 0.054 | 2.83x10-8 | Anthocyanin development in roots and stems, stress response-HORVU.MOREX.r2.2HG0088670.1 |
| TP3-GI | JHI-Hv50k-2016-198312 | 3H | 540936436 | 0.225 | 5.25x10-6 | HvVP1 |
| TP1-GE, TP1-GI, TP1-GI\_5D | JHI-Hv50k-2016-228853 | 4H | 9192492 | 0.397 | 1.97x10-6 | NRT1/PTR family protein |
| TP2-GI, TP2-GI\_5D, TP3-GI, TP3-GI\_5D | JHI-Hv50k-2016-229031 | 4H | 9491790 | 0.486 | 3.22x10-8 |
| TP3-GE | JHI-Hv50k-2016-229089 | 4H | 9768925 | 0.491 | 2.57x10-10 |  |
| All germination traits | JHI-Hv50k-2016-311497 | 5H | 475342665 | 0.358 | 1.86x10-42 | GRAM-containing/ABA-responsive protein, ISA3 |
| TP1-GE\_5D, TP1-GI, TP1-GI\_5D, TP2-GI | JHI-Hv50k-2016-311574 | 5H | 475453779 | 0.305 | 2.10x10-11 |
| TP1-GE | JHI-Hv50k-2016-311960 | 5H | 477497810 | 0.356 | 1.90x10-12 |
| TP4-GE\_5D | JHI-Hv50k-2016-315906 | 5H | 491911433 | 0.103 |  | Altered Abscisic acid signaling and drought tolerance |
| TP4-GE, TP5-GE | BOPA1\_5004-375 | 5H | 493200949 | 0.106 | 2.59x10-12 |  |
| TP4-GE, TP5-GE | JHI-Hv50k -2016-316599 | 5H | 493408279 | 0.104 | 1.26x10-14 |  |
| TP5-GE | SCRI\_RS\_19741 | 5H | 567309951 | 0.214 | 1.38x10-9 |  |
| TP5-GE,TP5-GE\_5D | BOPA1\_585-342 | 5H | 579812809 | 0.356 | 1.37x10-14 | Beta-glucosidase, Protein kinase family protein |
| TP1-GE, TP1-GI, TP1-GI\_5D | JHI-Hv50k-2016-513498 | 7H | 623659640 | 0.151 | 3.82x10-6 |  |

 \*Trait abbreviations: Preharvest sprouting (PHS), germination energy (GE), germination index (GI), GE\_5D (germination energy 5 Day),GI\_5D (germination index 5 Day), time point 1 (TP1), time point 2 (TP2), time point 3 (TP3), time point 4 (TP4), time point 5 (TP5)

\*\*MAF: Minor allele frequency

\*\*\*P-values below the Bonferroni cutoff (p=0.05) of 3.57x10-6 were considered significant

 Figure 1: Three-day germination energy (GE) best linear unbiased estimators (BLUEs). Facets show change in GE BLUEs over time within each family. Dotted lines indicate checks and gray lines are experimental lines ineach respective family.

Chart

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Figure 2: Three-day germination index (GI) best linear unbiased estimators (BLUEs). Facets show change in GI BLUEs over time within each family. Dotted lines indicate checks and gray lines are experimental lines in each respective family.

Chart

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Figure 3: Germination energy (GE) and germination index (GI) best linear unbiased estimators (BLUE) values based *HvAlaAT1* KASP marker (AlaAT\_L214F) haplotype at time point 2 (TP2) for each family in the winter barley population.

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**Section 2 Spring Barley**

Objective 2: Further characterizing the *SD2* locus in spring germplasm and screen a diverse set of European landraces to identify unique seed dormancy alleles.

Our 2019 progress report summarized the “GENETIC CHARACTERIZATION OF THE SD2 SEED DORMANCY LOCUS IN BARLEY**”** project. The genomic region around *SD2* (Seed Dormancy 2) has consistently been associated with malting quality traits and PHS in barley. At this locus, PHS resistance is typically associated with poor malting quality but the precise genetic nature of this relationship is unknown. A large effect mitogen-activated protein kinase kinase (*HvMKK3)* gene associated with PHS has been cloned at *SD2* (Nakamura et al., 2016) but a gibberellin oxidase gene, *HvGA20ox1,* that has been implicated in seed dormancy and PHS (Spielmeyer et al., 2004; Nagel et al., 2018) is located in the same region (~1.5 Mb proximal).  These two genes are close enough that previous genetic mapping studies may have identified them as a single large effect locus and were not able to differentiate separate effects. A Cornell spring two-row breeding population (CU, n=416) segregating at the *SD2* locus was genotyped with the Illumina 50K chip and a subset (n=306) was phenotyped in 2019 for PHS, grain dormancy, and germination rate. Lines with PHS resistance and high germination rate were identified that may have good malting quality. Genome-wide association (GWA) mapping suggested that the *SD1* locus, likely *HvAlaAT1* (Sato et al., 2016), and two distinct loci at *SD2*, putatively *HvGA20ox1* and *HvMKK3,* were contributing to phenotypic variation in germination energy and index.Nakamura et al. (2016) identified a remarkable 92 *HvMKK3* alleles in wild and cultivated barley. Vetch et al. (2020) did not find the N260T mutation identified by Nakamura et al. (2016) as the causal polymorphism in cv. Azumamugi but described four additional alleles in North American spring malting barley germplasm, identifying E165Q as the primary non-dormant *HvMKK3* allele.

Materials and methods

To further investigate genetic effects at *SD2*, we phenotyped the full CU population in 2020 in two locations in Ithaca, NY. A panel of 86 predominantly European two-and six-row spring landraces, initially assembled by the John Innes Centre (JIC, Norwich, UK) for disease resistance screening, was also phenotyped for PHS in 2019 and 2020 and phenotyped for germination traits in 2020. An additional 20 spring hulless, or naked, barley lines and the six-row non-dormant cv. ‘Morex’ and dormant cv. ‘Steptoe’ checks were also phenotyped for PHS and germination traits in 2020. A total of 523 lines were phenotyped in 2020. PHS measurements were taken for a subset of this population and germination trait phenotypes were recorded for all lines at six timepoints from one week to three months post-physiological maturity. PHS and germination trait phenotyping methods are the same as described in the winter barley section of this report.

The JIC lines, Morex, and Steptoe were Sanger sequenced by the USDA Cereal Crops Research Unit (CCRU) for *HvAlaAT1* and *HvMKK3* (Tables 3 and 5). CCRU also Sanger sequenced *HvGA20ox1* for 81 spring and winter barley lines that had historic PHS phenotypes.  Mutations in non-coding regions of *HvGA20ox1* were identified but no non-synonymous coding regions mutations were detected (Table 4). A003GA20ox1,which was carried by most PHS susceptible lines, was also present in PHS resistant winter six-row naked barley lines as well as Steptoe, and thus was not highly correlated with PHS.

We previously reported development of a high-throughput Kompetitive Allele Specific Primer (KASP) marker AlaAT1\_L214F for the causal mutation in *HvAlaAT1* discovered by Sato et al. (2016). We also developed KASP assays for a SNP in the 5’ UTR of *HvGA20ox1* (GA20ox1\_331\_5UTR), the E165Q mutation in *HvMKK3* identified in Vetch et al. (2020) (MKK3\_E165Q), and the JHI-Hv50k-2016-367342 50k marker, which is 152 bp proximal to *HvMKK3* and was highly correlated (0.96) with the R350G mutation in *HvMKK3* identified by Vetch et al. (2020) in the Sanger sequenced JIC lines. The MKK3\_E165Q marker should only be used in inbred lines as the non-dormant allele appears in a heterozygote cluster distinct from the dormant allele. KASP primers and protocols will be published in a forthcoming manuscript and are available upon request. The CU/JIC population was genotyped for each KASP marker. All lines were genotyped with the 50k Illumina Infinium iSelect SNP array at the USDA Small Grains Genotyping Lab in Fargo, ND. After filtering poor quality markers and minor allele frequency below 0.05, 14,017 polymorphic markers remained and were used for GWA. The *GAPIT* R package (Tang et al., 2016) was used for GWA. Multi-locus mixed models (MLMM) were fit for PHS, germination energy, and germination index at six after-ripened time points. This model is simpler than the model we used last year, FarmCPU, and produces somewhat more conservative results. Marker-trait associations (MTA) with p-values below the Bonferroni cutoff (p=0.05) of 3.57e-6 were considered significant.

Results

MTA associated with *HvMKK3* and *HvAlaAT1* were detected across time points for germination energy and germination index but no MTA were detected for *HvGA20ox1* (Table 2). Markers JHI-Hv50k-2016-366325, SCRI\_RS\_10702, and SCRI\_RS\_193456 were in high linkage disequilibrium (LD) with JHI-Hv50k-2016-367342 and have very similar MAF, indicating they were likely identifying the same locus. MKK3\_E165Q and JHI-Hv50k-2016-367342 had MAF of 0.19 and 0.38, respectively, and the non-dormant MKK3\_E165Q allele was always present with a non-dormant allele of JHI-Hv50k-2016-367342, similar to E165Q and R350G in Vetch et al. (2020). Thus, combinations of MKK3\_E165Q and JHI-Hv50k-2016-367342 appear to identify three alleles of *HvMKK3* with differing effects on seed dormancy.

Our GWA results support the role of the highly non-dormant E165Q (A001MKK3 in this study)allele in increasing PHS and additionally indicate a major role of this allele on germination index. Lines with A001MKK3 had high PHS, low primary dormancy, and high germination index regardless of dormant alleles at *HvAlaAT1* or *HvGA20ox1*. Our results strongly suggest that other *HvMKK3* alleles also affect primary dormancy and germination rate.  We labeled the A003MKK3 allele identified by the JHI-Hv50k-2016-367342 marker (R350G/N383D in Vetch et al., 2020) as non-dormant despite its association with PHS resistance because it was also associated with low primary dormancy and increased germination rate. A dormant *HvMKK3* allele, A002MKK3, conferred PHS resistance, high primary dormancy, and decreased germination rate. Two other *HvMKK3* alleles, A004MKK3 and A005MKK3, were identified in JIC but their effects are not known.  A001MKK3 was found in Klages by Vetch et al. (2020). Klages was derived from Betzes/Domen and is in the pedigree of many current varieties with A001MKK3. Domen, derived from OpalB/Maskin, likely carries A001MKK3 (sequencing ongoing).OpalB is a selection from the Danish lineOpal, which was sequenced by Nakamura et al. and does not carry A001MKK3. No *HvMKK3* sequence for Maskin, a Norwegian six-row spring landrace (Aikasalo, 1988), is available but A001MKK3 was identified in two other Norwegian six-row spring landraces in the JIC, ‘Kagelkorn’ and ‘Tamparkorn’. Sequences from ‘Harrington’, ‘Steptoe’, 36 unique *HvMKK3* alleles detected in cultivated barley by Nakamura et al. (2016), and the twenty barley pan-genome lines (Jayakodi et al., 2020) were aligned. A001MKK3 was only observed in ‘Hockett’, ‘Harrington’, and a Russian accession ‘Caucasus’ (Hap\_033, OU ID U388).  A001MKK3 was primarily found in varieties from breeding programs in western Canadian, Washington, Montana, and Idaho by Vetch et al. (2020) while A002MKK3 and A003MKK3, were present in a wider range of germplasm from North America and Europe in our study. A001MKK3 seems to be relatively rare globally but is enriched in North American malting germplasm. ‘Canadian-style’ malting quality is highly preferred by North American adjunct brewers and is characterized by high enzyme activity, free amino nitrogen (FAN), and low beta-glucan (Edney et al., 2013). Varieties with ‘Canadian-style’ malting quality frequently have PHS issues and A001MKK3 may be partially responsible for high adjunct brewing performance and high PHS risk. European and North American craft brewing styles rarely use adjuncts and have different preferences for malting quality profiles, generally favoring lower enzyme levels, FAN, and protein than adjunct brewing. Combined with favorable malting quality QTL, the A002MKK3 and A003MKK3 alleles may help provide effective protection against PHS without compromising malting quality for craft malting and brewing markets.

Epistatic interactions between *HvMKK3* alleles, *HvAlaAT1*, and possibly *HvGA20ox1* were observed (Figures 4 and 5). Dormant *HvAlaAT1* alleles had minimal impact on PHS but increased primary dormancy length and decreased germination index. These results are consistent with previous studies that implicated *HvAlaAT1* in prolonged seed dormancy. Although no significant MTA for *HvGA20ox1* were identified, GA20ox1\_331\_5UTR was associated with germination index in a few haplotype pairs, notably DNN/DDN. The LD between GA20ox1\_331\_5UTR and MKK3\_E165Q was 0.59, which should have been sufficiently low for GA20ox1\_331\_5UTR detection using the MLMM model if there was a large effect associated with that marker. The putative non-dormant allele of *HvGA20ox1*, A003GA20ox1, was linked with A003MKK3 for the vast majority of the CU population and may have limited the ability to detect genetic effects in the more modern germplasm. This linkage may have also created long-range LD that gave the appearance of two distinct loci at *SD2* in the 2019 results.  We previously reported a recombination between *HvGA20ox1* and *HvMKK3* in the *SD2* region but further investigation determined that putative recombinant lines had incorrect pedigrees and were not actual recombinants. Accurate estimation of genetic effects of certain haplotypes (NNN, DND, DNN) are limited in this study since many lines carrying those haplotypes with limited replication in JIC lines that may hold additional small effect seed dormancy QTL. The repeated significance of the AlaAT\_L214F and MKK3\_E165Q markers validate the effects of *HvAlaAT1* and *HvMKK3* in spring malting barley reported by other authors.

To further test if *HvGA20ox1* has an effect on PHS in less structured North American germplasm, we are currently genotyping the S2MET population (Neyhart et al., 2019), which is composed of two-row spring breeding lines from Montana State University, USDA Aberdeen, North Dakota State University, Washington State University, and the University of Minnesota, with the seed dormancy KASP markers. The S2MET was phenotyped for PHS at Cornell in 2015 and 2016 and genotyped with GBS markers. GWA for PHS in this population also suggests the influence of multiple *HvMKK3* alleles but indicates *HvGA20ox1* may have an effect on PHS. Results will be shared in a supplemental report before April 1, 2021. Accompanying this supplement will also be the results of a time series analysis of germination percentage and index, both as a validation of the markers identified in the single time point association models mentioned here, but also to potentially identify more novel dormancy QTL. A QTL by environment modeling study that is investigating the response of different seed dormancy haplotypes to environmental variables is also nearing completion.

Table 2: Summary of 2020 genome-wide association studies for PHS and germination traits in the CU/JIC population. Germination energy (GE) and germination index (GI) were phenotype at six timepoints (TP) after physiological maturity, ranging from one week to three months.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Trait\*** | **Marker** | **Chr** | **Position** | **MAF\*** | **Genes of Interest** |
| GE\_TP1, GE\_TP2, GE\_TP3, GI\_TP1, GI\_TP2, GI\_TP3, GI\_TP4 | AlaAT\_L214F | 5H | 442160000 | 0.327 | *HvAlaAT1* |
| PHS, GE\_TP1, GI\_TP3, GI\_TP2, GI\_TP3, GI\_TP4 | MKK3\_E165Q | 5H | 596729750 | 0.191 | *HvMKK3* |
| GE\_TP1, GE\_TP2, GE\_TP3, GI\_TP1, GI\_TP2, GI\_TP3, GI\_TP4 | JHI-Hv50k-2016-367342 | 5H | 596729543 | 0.380 | *HvMKK3* |
| GI\_TP6 | JHI-Hv50k-2016-366325 | 5H | 598980001 | 0.388 | *HvMKK3* |
| GE\_TP3 | SCRI\_RS\_10702 | 5H | 596742751 | 0.388 | *HvMKK3* |
| GI\_TP6 | SCRI\_RS\_193456 | 5H | 596540049 | 0.378 | *HvMKK3* |

  \*Trait abbreviations: Preharvest sprouting (PHS), Germination energy (GE), germination index (GI), time point 1 (TP1), time point 2 (TP2), time point 3 (TP3), time point 4 (TP4), time point 5 (TP5), and time point 6 (TP6)

\*\*MAF: Minor allele frequency

\*\*\*P-values below the Bonferroni cutoff (p=0.05) of 3.57x10-6 were considered significant

Table 3: Summary of *HvAlaAT1* alleles. N indicates the number of JIC and winter and spring breeding lines with each allele. Bp position indicates the location of the polymorphism in the coding sequence of the gene and Nuc. indicates the nucleotides present at each polymorphism site.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  |  | **Gene** | *HvAlaAT1* | |
|  |  | **Exon/Intron** | Exon 9 | Exon 10 |
|  |  | **Mutation type** | missense | missense |
|  |  | **bp position** | 222 | 467 |
| **Allele** | **n** | **Phenotype** | **Nuc.** | **Nuc.** |
| A001AlaAT1 | 33 | dormant | C | C |
| A002AlaAT1 | 109 | non-dormant | G | C |
| A003AlaAT1 | 1 | unknown | C | A |

Table 4: Summary of *HvGA20ox1* alleles. N indicates the number of JIC and winter and spring breeding lines with each allele. Bp position indicates the location of the polymorphism in the coding sequence of the gene and Nuc. indicates the nucleotides present at each polymorphism site.

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | **Gene** | *HvGA20ox1* | | | | | | | | |
|  |  | **Exon/Intron** | 5' UTR | | | Exon 1 | | Intron 1 | Exon 2 | | |
|  |  | **Mutation type** | n/a | n/a | n/a | silent | silent | n/a | silent | silent | missense |
|  |  | **bp position** | 284 | 316 | 331 | 458 | 764 | 954 | 1216 | 1381 | 1480 |
| **Allele** | **n** | **Phenotype** | **Nuc.** | **Nuc.** | **Nuc.** | **Nuc.** | **Nuc.** | **Nuc.** | **Nuc.** | **Nuc.** | **Nuc.** |
| A001GA20ox1 | 21 | dormant | T | T | C | C | G | - | C | G | A |
| A002GA20ox1 | 3 | dormant | C | A | C | C | G | - | C | G | A |
| A003GA20ox1 | 14 | non-dormant | C | A | G | A | C | G | T | C | A |
| A004GA20ox1 | 25 | dormant | C | A | C | C | G | - | T | G | A |
| A005GA20ox1 | 2 | non-dormant | C | A | G | A | C | G | T | C | T |

Table 5: Summary of *HvMKK3* alleles. N indicates the number of JIC and winter and spring breeding lines with each allele. Bp position indicates the location of the polymorphism in the coding sequence of the gene and Nuc. indicates the nucleotides present at each polymorphism site.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | **Gene** | *HvMKK3* | | | | |
|  |  | **Exon/Intron** | Exon 3 | Exon 4 | Exon 7 | Exon 7 | Exon 8 |
|  |  | **Mutation type** | missense | missense | missense | silent | missense |
|  |  | **bp position** | 189 | 498 | 476 | 512 | 32 |
| **Haplotype** | **n** | **Phenotype** | **Nuc.** | **Nuc.** | **Nuc.** | **Nuc.** | **Nuc.** |
| A001MKK3 | 5 | highly non-dormant | C | G | G | T | G |
| A002MKK3 | 53 | dormant | G | G | C | T | A |
| A003MKK3 | 15 | non-dormant | G | G | G | T | G |
| A004MKK3 | 2 | unknown | G | G | G | G |  |
| A005MKK3 | 8 | unknown | G | T | C | T | A |

Figure 4. Distribution of preharvest sprouting best linear unbiased estimators (BLUEs) in CU/JIC. Seed dormancy haplotypes were defined as the combination of alleles at *HvAlaAT1*, *HvGA20ox1*, and *HvMKK3* where “N” indicates a non-dormant allele and “D” indicates a dormant allele. “N\*” was used to indicate the presence of the *HvMKK3* E165Q mutation. The marker name columns indicate the nucleotides present at each site. Haplotypes that share a letter in the TukeyHSD did not have significantly different means (a=0.05).

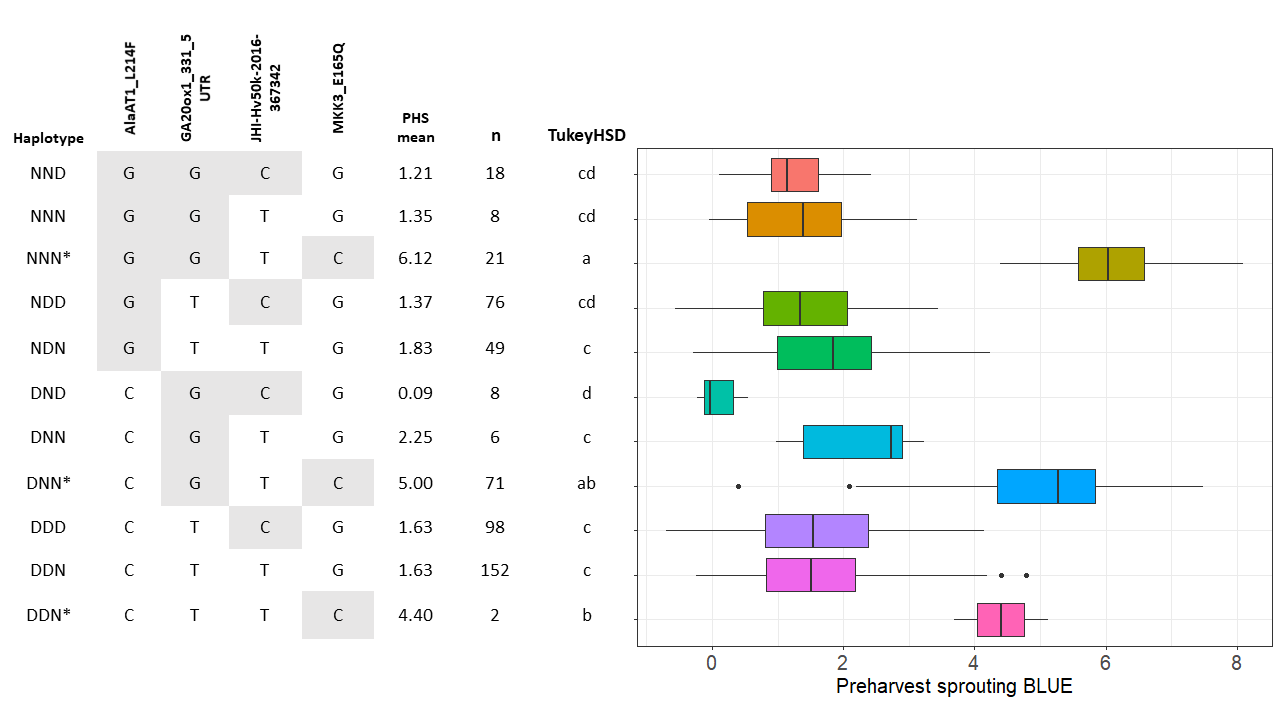
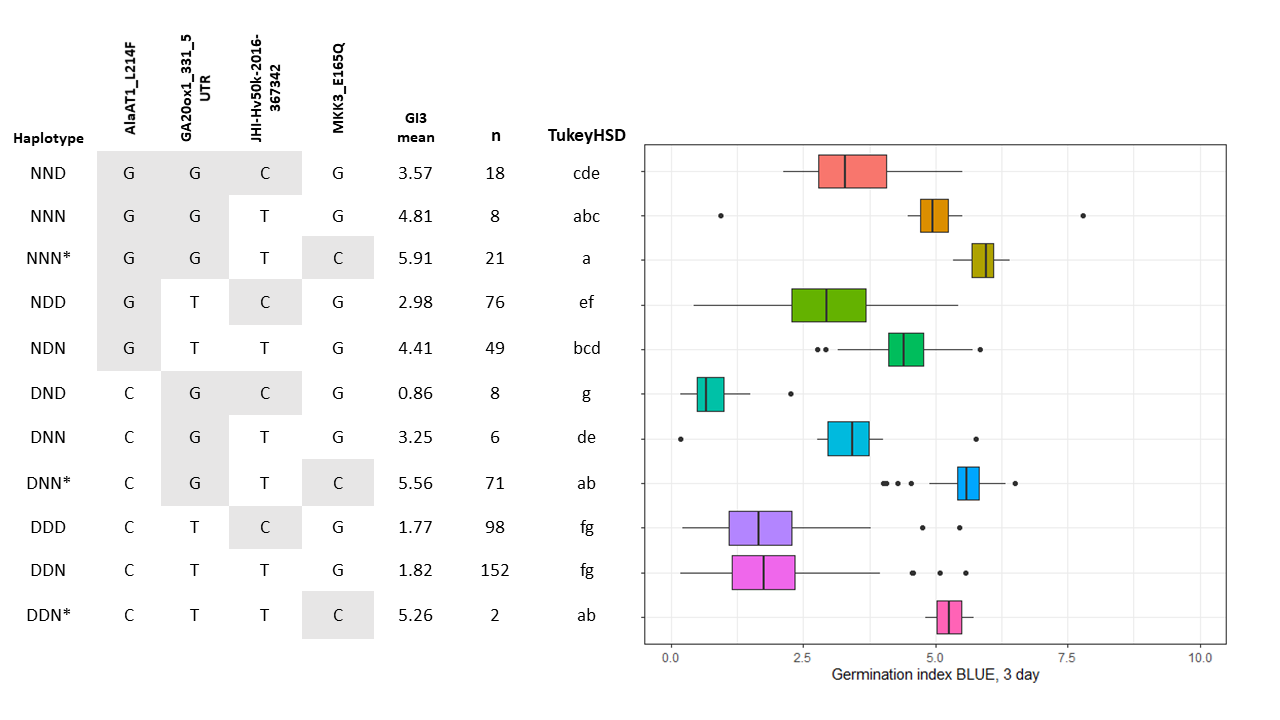


Figure 5: Distribution of germination index best linear unbiased estimators (BLUEs) in CU/JIC at six days after physiological maturity. Seed dormancy haplotypes were defined as the combination of alleles at *HvAlaAT1*, *HvGA20ox1*, and *HvMKK3* where “N” indicates a non-dormant allele and “D” indicates a dormant allele. “N\*” was used to indicate the presence of the *HvMKK3* E165Q mutation. The marker name columns indicate the nucleotides present at each site. Haplotypes that share a letter in the TukeyHSD did not have significantly different means (a=0.05).



**Other barley research**

-Two-row winter malting barley breeding program evaluating winter double haploid population and RIL population in augmented design in yield plots at two locations

-Multi-purpose organic naked barley research NAM F2 selection experiment funded by Organic Research and Education Initiative (OREI)

-Value added grains experiment funded by the Organic Research and Education Initiative (OREI) lead by Mark Sorrells

**Project personnel**

Mark Sorrells, David Benscher, Amy Fox, James Tanaka, Daniel Sweeney, Karl Kunze, Travis Rooney

**Recent publications**

Sweeney, D.W., J. Rutkoski, G.C. Bergstrom, M.E. Sorrells, 2020. A connected half‐sib family training population for genomic prediction in barley. *Crop Science* 60: 262– 281. [https://doi.org/10.1002/csc2.2010](https://doi.org/10.1002/csc2.20104)

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