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ORIGINAL ARTICLE

Crop Economics, Production, and Management

Effects of genotype and environment on productivity and quality in Californian malting barley

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Abstract

Malting barley (*Hordeum vulgare* L.) productivity and grain quality are of critical importance to the malting and brewing industry. In this study, we analyzed 12 malting barley genotypes across 8 locations in California and 3 years (2017–2018, 2018–2019, and 2020–2021). The effects of genotype (*G*), location (*L*), year (*Y*), and their interactions were assessed on grain yield (kg ha^{-1}), grain protein content (%), individual-grain weight (mg), thousand kernel weight (TKW; g), grain size (plump and thin; %), onset gelatinization temperature (GT; temperature at which starch starts to gelatinize), peak GT, offset GT, difference between onset and peak GT, and difference between peak and offset GT. *L*, *Y*, and their interaction explained the largest variance for all traits except TKW, peak GT, and difference between onset and peak GT, for which *G* explained the largest variance. Yield and plump (%) were weakly negatively correlated with onset and peak GT (Pearson's *r* of −0.15 to −0.21) but showed a positive correlation with the difference between peak and offset GT (Pearson's *r* of 0.37 and 0.36). The 2020–2021 samples formed partially distinct clusters in principal component analysis, mainly discriminated by high percentage of thins and high onset GT. These findings illustrate the key roles of *G*, *L*, and *Y* in determining malting barley productivity and quality.

1 | INTRODUCTION

The barley belt is a term used to describe the primary barley production region in the United States, spanning from Washington State in the west to North Dakota in the east (American Malting Barley Association [AMBA], 2022). In California, malting barley growing regions are primarily located in the Sacramento and San Joaquin Valleys and south-Central Coast.

Abbreviations: AMBA, American Malting Barley Association; ASBC, American Society of Brewing Chemists; B, block; GT, gelatinization temperature; *G*, genotype; GPC, grain protein content; IGW, individual-grain weight; LMEs, linear mixed effects; *L*, location; TKW, thousand kernel weight; UC, University of California; *Y*, year.

Production of malting barley in California typically makes use of "spring" varieties (i.e., not having a vernalization requirement) that are planted in fall and harvested in summer (Jackson et al., 2006; Lazicki et al., 2016). In 2021, approximately 20% of barley produced in California was grown in the Tulelake basin (Siskiyou County) as a rotation crop with potato (*Solanum tuberosum* L.), onion (*Allium cepa* L.), and alfalfa (*Medicago sativa* L.; NASS, 2023). In the Sacramento and San Joaquin Valleys and the Southern desert region, barley is grown predominantly as a rotation crop. These environments form part of the Central Valley and Imperial Valley of California with Mediterranean, semiarid, and arid desert type climate profiles. As malting barley is often grown as a rotation crop in a wide range of conditions (Kanter et al., 2021), it is critical to understand the impact of location on malting barley grain quality. Mediterranean climates are known for their temporal variability, driven by hot and dry summers and rainy winter spells with more frequent weather extremes (Hochman et al., 2021; Nelsen & Lundy, 2020). Despite these variable conditions, field crop acreage in California is projected to increase with increased advocacy of water-limited winter cropping systems in light of the recent Sustainable Groundwater Management Act (Peterson et al., 2022). However, the contributions of warming and increased incidents of drought to grain quality are still unknown.

Malting barley productivity is directly linked to the sustainable supply of grain to malthouses, and grain quality can impact malting and brewing efficiencies, beer quality, and flavor (AMBA, 2021; Bamforth, 2006). Previous studies have found the interaction of genotype and environment to play an important role in barley yield and quality in multiple production regions worldwide (Bantayehu, 2013; Fekadu et al., 2023; Laidig et al., 2017; Nielsen & Munck, 2003; Przulj et al., 2014) and in the United States (Choi et al., 2020; Zhou et al., 2020). However, those studies measured either agronomic traits or grain quality traits stipulated by industry standards. To understand the impacts of *G*, *L*, and *Y* on downstream processing outcomes during brewing, it is important to consider more in-depth traits relating to starch gelatinization.

Grain of malting barley is typically composed of 50%–68% starch (Newman & Newman, 1992; Patindol et al., 2012; You & Izydorczyk, 2007). Barley starch content and composition play an important role during the mashing stage of brewing (Briggs, 1998). During mashing, starch is hydrolyzed to fermentable sugars such as maltose and maltotriose (which are extracted into the wort and later fermented by yeasts to produce beer). However, for enzymes to efficiently hydrolyze starch, starch must be gelatinized. Starch granules are gelatinized during mashing within a certain temperature range, indicated by onset, peak, and offset gelatinization temperatures (GT). In high-quality barley, the start of solubilization would be as low as 56°C (onset) and end around 65°C (offset). However, in barley that has been stressed due to high temperature or drought during grain-fill, the temperature range could be higher (Gous et al., 2015; Myllärinen et al., 1998). Hydrolysis is characterized by swelling of the starch granules within the endosperm and further gelatinization that typically occurs between 60 and 65°C in malting barley. This GT range does not change substantially between raw and malted barley, but there is a slight increase due to the malting process (Langenaeken et al., 2019). Two families of enzymes, namely, α and β-amylases, also play an important role in catalyzing this starch gelatinization. However, if the starch GT exceeds 65°C (as industry mashing protocol is set at 65°C), β-amylase is rapidly inactivated, which has been found to reduce brewing efficiency (American Society of Brewing Chemists [ASBC], 2011a; Evans et al., 2003). Hence, starch GT can serve as an indicator of malting barley quality and brewing performance.

Starch GT range in malting barley is affected by several factors, such as starch granule size (Karlsson et al., 1983), starch granule packing (Fox et al., 2007), ratio of amylose to amylopectin (respectively, the linear and branched-chain glucose polymers that compose starch), total amylose content (Fredriksson et al., 1998; Källman et al., 2015), grain protein content (GPC; %) (Wenwen et al., 2019), and grain weight (Kandic et al., 2019). Protein content could influence GT due to starch-protein interactions in the endosperm matrix, which inhibit the swelling of starch granules during mashing (Wenwen et al., 2019). Finally, a positive correlation between grain weight and starch GT has also been reported (Kandic et al., 2019).

Previous studies have reported substantial variation in starch GT among multiple genotypes of malting barley (Gujral et al., 2013; Jaiswal et al., 2014; Pycia et al., 2015). Other studies have found that location (Fox et al., 2001), year (Przulj et al., 2014), and environmental factors, such as drought stress (Gous et al., 2015), also affect starch GTs. However, these studies were not designed to include multiple locations,

Core Ideas

- Genotype, location, and year variably explain quality traits—for example, grain protein content, gelatinization temperature.
- The $L \times Y$ interaction explained the largest variance for GPC and yield.
- G and $L \times Y$ (and Y for onset) explained the largest variance in onset, peak, and offset GT.
- The 2020–21 samples formed partially distinct clusters, segregated by high thins and onset GT.
- Plumper grains had a lower onset GT but a larger difference between peak and offset GT.

years, and genotypes. In all cases, up to two out of the three were varied, while keeping the third variable constant. A multi-environment study has been conducted in California to assess yield performance in wheat (George & Lundy, 2019), but malting barley and quality traits have not received the same level of attention in this region to date. A major US genome-wide association study identified markers exhibiting significant associations with multiple malting barley quality traits (Mohammadi et al., 2015). These instances of potential pleiotropy could make genomics-assisted selection for a full suite of quality traits challenging for breeders. That study also found that the marker-trait associations detected in individual (sub)regional programs were largely distinct from those detected in other programs, and that analyzing a combined panel across programs resulted in loss of 33 out of 52 marker-trait associations (and the detection of eight new associations in the combined panel) in two-row barley. Thus, examinations of quality on a (sub)regional basis will continue to be important to breeding (and agronomic) efforts.

This study aims to elucidate the complexity of maintaining malting barley productivity and quality in the context of inter-annual temperature and precipitation variability. We assessed the following traits in spring malting barley varieties grown in California: grain yield (kg ha^{-1}), GPC (%), individual-grain weight (IGW; mg), thousand kernel weight (TKW; g), grain size (percentage of plump and thin grains), and onset GT, peak GT, offset GT, difference between onset and peak GT, and difference between peak and offset GT (°C). We examined whether genotype (*G*), location (*L*), and/or year (*Y*) play a more important role in affecting the aforementioned traits using samples from a multi-environment variety trial. Furthermore, we examined correlations between these malting barley productivity and quality traits, with an aim to generate hypotheses at the molecular/compositional level. Variation in barley productivity and quality traits arising from *G*, *L*, and/or *Y* combinations is leveraged herein to understand relationships among traits affecting end usability for maltsters and brewers.

2 | MATERIALS AND METHODS

2.1 | Multi-environment variety trial

The barley grain samples analyzed in this study were harvested from variety trials conducted in the 2017–2018, 2018–2019, and 2020–2021 growing seasons, by the University of California (UC) Small Grains Research team. For example, the growing season designated as "2017–2018" was planted in fall of 2017 and harvested in summer of 2018. These trials were planted in a randomized complete block design with four replications per location, at each trial location (Nelsen & Lundy, 2020; Nelsen, Levinson, et al., 2021; UC-ANR, 2020). Grain from one out of the four replicates from each location was used for grain quality analysis. Twelve genotypes (nine varieties and three experimental lines) of two-row spring malting barley that were developed in the United States were included in this study, which were grown in eight field sites within California (Table S1; Figure S1). The plots were 3.65 m by 6 m and established with a 3.65 m grain drill in the fall season (Table S1); fall planting is in line with common agronomic practice in California (Jackson et al., 2006; Lazicki et al., 2016). A seeding rate of approximately 2.2 million seeds per hectare was used across seasons (Nelsen & Lundy, 2020). These field trials were conducted in different areas of the state where malting barley is typically grown, with varying management practices based on the initial soil moisture and nitrogen (N) levels at each location–year (*LY*). Grain was harvested using a Wintersteiger Classic small plot combine, weighed, and cleaned (to collect subsamples that were used in the grain quality analyses described herein) prior to final yield calculation (in kg ha^{-1}) per plot, as described previously (Nelsen & Lundy, 2020). Calculated grain yields for each replicate plot for a given genotype within an *LY* combination (including one additional year in the Yolo 2 location that was not analyzed for grain quality) were used for Finlay–Wilkinson (FW) regression, linear mixed effects (LMEs) modeling, and post hoc tests. Average yields for each genotype–location–year (*GLY*) combination were used for the correlation matrix and principal component analysis (PCA).

Average TKW values from multiple plot replicates were used for the small number of *GLY* combinations for which this trait was measured on multiple replicates; otherwise, the data from one replicate was used for all analyses. Grain samples from one replicate plot per *GLY* combination were used for measurement of all other quality traits (Table S3). The precipitation and temperature data (Tables S1 and S5) were obtained from the California weather web-tool (Nelsen, Merz, et al., 2021).

2.2 | Starch gelatinization (differential scanning calorimetry)

In preparation for an analysis of starch gelatinization, the grain samples were ground in a Disc Mill (Buhler DLFU, Buhler AG, CH-Uzwil) using the fine (0.2 mm particle size) setting into barley flour. Differential scanning calorimetry was then conducted using a modified procedure described previously (Fox et al., 2019). Briefly, 2 mg (±0.15 mg) of barley flour was weighed into a Tzero aluminum pan (TA Instruments), to which deionized water was added until the total mass was 5 mg (±0.15 mg). The pan was then dry sealed. The blank used for the testing was an empty pan, which was also dry sealed. Using a DSC-250 differential scanning calorimeter (TA Instruments), the heating regimen started with an

initial temperature of 40°C followed by a ramp-up to 75°C with 5°C min^{-1} increments. Onset temperature, peak temperature, and offset temperature were measured over a peak integration of 55–75°C using the Trios v4.2.136612 software program (TA Instruments). Enthalpy (J g^{-1}) and time to peak temperature (min) were also recorded but not analyzed in this study.

2.3 | Grain weight and size

For the 2017–2018 and 2018–2019 years, 50 grains were taken from a representative sample, and each grain was weighed on a precision balance. The same grains were then measured using a vernier caliper, and length and breadth measurements were recorded in mm (comparable to industry standard method). This method was repeated for all grain samples in duplicate and was used to measure plump and thin grains (%) in these seasons due to the limited grain quantity that was available. For the 2020–2021 year, plump and thins (%) were measured using the industry standard method (ASBC, 2012). One hundred grams (±0.1 g) of sample was passed through four consecutive sieves (2.78 mm [7/64 in.], 2.38 mm [6/64 in.], 2.18 mm [5.5/64 in.], and 1.98 mm [5/64 in.]) using a sieve shaker (Sortimat Sample Grader K4, Pfeuffer) for 3 min (±10 s). The sample collected in each sieve was weighed, and the percentages of sample from the 2.78 and 2.38 mm sieves were recorded as plump and thins (%), respectively. TKW was measured by counting, collecting, and weighing 200 seeds from each sample with an electronic seed counter (ASBC, 2011b). Weights were converted proportionally to TKW.

2.4 | Grain protein content

GPC (%) and moisture (%) were quantified using the near infrared reflectance (NIR) grain analyzer (Infratec, FOSS) using a preexisting barley calibration. GPC and moisture % results obtained for a randomized subset of samples were further validated using combustion with thermal conductivity (TruSpec CN Analyzer; AOAC Official Method 972.43, 2006) conducted by the UC Davis Analytical Lab (Table S6).

2.5 | Statistical analysis

2.5.1 | Finlay–Wilkinson (FW) regression

FW regression (Finlay & Wilkinson, 1963) was performed using LY means and genotype as covariates in a linear model (Equation 1 for yield, and Equation 2 for all other traits). The model was fitted in R 4.2.1 (R Core Team, 2020) and R Studio version 2022.07.1 builds 485 (RStudio Team, 2022) using the *lm()* function within the *lme4* package (Bates et al., 2015) and *emtrends()* function within the *emmeans* package (Lenth et al., 2023; Searle et al., 1980):

$$y_{ijr} \sim \mu + g_i h_j + \varepsilon_{ijr} \quad (1)$$

$$y_{ij} \sim \mu + g_i h_j + \varepsilon_{ij} \quad (2)$$

where y_{ijr} represents the yield value of the rth replicate for genotype i in environment j (where j represents the *LY* combination), and y_{ij} represents the trait value for genotype i in environment j. μ is the grand mean, g_i is the main effect of the ith genotype, h_j is the main effect of the jth environment, and ε_{ijr} (for yield) or ε_{ij} (for all other traits) is the error term (Lian & de los Campos, 2015). For yield, values for each plot replicate within a *GLY* combination were used. For TKW, average values across multiple replicates per *GLY* combination were used for the small number of *GLY* combinations for which this trait was measured on multiple replicates; otherwise, the data from one replicate was used. For all other traits, the values measured on one replicate per *GLY* combination were used.

Slopes were considered to be significantly different than one if their confidence interval, as calculated using the *emtrends()* function in the *emmeans* package (Lenth et al., 2023), did not contain one. Slopes were only described in the text for genotypes that were observed in at least half of the environments in this study. For plots depicting the FW regression, the environmental effect (regression estimates for each *LY* combination across all genotypes; Lian & de los Campos, 2015) was plotted in the *X*-axis and genotype performance (regression estimates for each genotype within each *LY* combination) in the *Y*-axis.

2.5.2 | Modeling

Yield

For estimation of variance components, an LMEs model was run for yield from each replicate plot within a *GLY* combination, with the inclusion of a block effect nested within *LY* as shown in the following equation:

$$y_{ijkz} \sim \mu + g_i + l_j + s_k + g_i l_j + g_i s_k + l_j s_k + g_i l_j s_k + b_z(l_j : s_k) + \varepsilon_{ijkz} \quad (3)$$

where y_{ijkz} represents the response measured for genotype i, in location j, in year k, within block z, and μ is the grand mean. g_i is the main effect of the genotype, l_j is the main effect of the location, s_k is the main effect of the year, b_z is the block effect nested in location and year, g_i l_j is the interaction of genotype

and location, and so on. ε_{ijkz} is the residual term. All predictor variables were inputted as random effects (random intercepts and fixed slopes) via the *lmer()* function in the *lme4* package (Bates et al., 2015).

For purposes of mixed analysis of variance (ANOVA) (solely to determine which post hoc tests were appropriate to conduct) and post hoc tests, a model that combined the *L* and *Y* terms into a generic environment (*E,* or "*LY*") term (Equation 4) was fit using *lmer()* with all terms as fixed effects except for block (nested in *LY*), which was fit as a random effect. This combining of *L* and *Y* was conducted to represent individual growing environments, ensure appropriate nesting of block in mixed ANOVA, only conduct comparison of means for *LY* combinations that were tested in the present study, and improve tractability of examining the results of pairwise comparisons (rather than comparing each *G*, *L*, and *Y* combination):

$$y_{imz} \sim \mu + g_i + e_m + g_i e_m + b_z(e_m) + \varepsilon_{imz} \quad (4)$$

p-Values for fixed effects in this model were obtained using the *mixed*() function in the *afex* package (Singmann et al., 2023) using the default settings (Kenward–Roger approximation), as in Dia et al. (2017). We only conducted post hoc tests for the highest-order term that was significant for a given variable. In the case of a three-way interaction exhibiting significance, we conducted a comparison of means for all genotypes (*G*) within a given *LY* combination, and for all LYs for a given genotype (*G*). Pairwise comparison of means was conducted using the *emmeans()* function in the *emmeans* package (Lenth et al., 2023; Searle et al., 1980) using list(pairwise ~ *G|LY*) or list(pairwise ~ *LY|G*) and adjust = "Tukey." Connecting letters reports were generated using the *cld*() function in the *multcomp* package (Hothorn et al., 2008) and used to identify means that were significantly different from each other ($\alpha = 0.05$).

Grain quality traits

The LMEs model was run using the *lm*() function in the *lme4* package (Bates et al., 2015) for all grain quality traits analyzed from one replicate per *GLY* combination, except for TKW where averages from multi-replicate data were used where available. The dataset, including data from 12 genotypes, 8 locations, and 3 seasons (2017–2018, 2018–2019, and 2020–2021), was used for this analysis. The variance components were estimated using an LMEs model (Equation 5). Mixed ANOVA was conducted using the *aov*() function (R Core Team, 2020) followed by the comparison of means via the Tukey–Kramer post hoc test (which was used due to unequal sample sizes; unbalanced was set to TRUE) using the *HSD.test*() function in the *agricolae* package (de Mendiburu., 2021) for the same Equation (5). We only conducted the Tukey–Kramer post hoc test for the highest-order term that was significant for a given variable; for example, if the location:year interaction term and main effect of genotype were significant, we fit the Tukey–Kramer post hoc test for those terms but did not do so for the main effects of each of location and year. Means that were significantly different from each other ($\alpha = 0.05$) in pairwise comparisons were identified using connecting letter reports from this analysis. We did not describe in the text any comparisons of levels that were not ever directly compared to each other (e.g., two genotypes that were not tested in any of the same LYs, or two locations that were each only tested in 1 year and that were tested in a different year from each other):

$$y_{ijk} \sim \mu + g_i + l_j + s_k + g_i l_j + g_i s_k + l_j s_k + \varepsilon_{ijk} \quad (5)$$

where y_{ijk} represents the response measured for genotype *i*, in location *j*, in year *k* and μ is the grand mean. g_i is the main effect of the genotype, l_j is the main effect of the location, s_k is the main effect of the year, and so on. ε_{ijk} is the residual term. All predictor variables were inputted as random effects (random intercepts and fixed slopes) for the LMEs model and fixed effects for the mixed ANOVA.

2.6 | Data visualization

Figure 1 was created using the *ggplot2* (Wickham, 2016), *agricolae* (de Mendiburu & Yaseen, 2020), *datasets* (R Core Team, 2020), and *reshape2* (Wickham, 2007) packages to visualize the responsiveness of each genotype across environments (LYs) for the measured traits using FW regression. Figure 2a (correlation matrix) was created using the *ggplot2* (Wickham, 2016), *corrplot* (Wei & Simko, 2021), and *tidyverse* (Wickham et al, 2019) packages. PCA was performed on the full dataset using the *prcomp* function with corresponding biplots (Figure 2b, c and Figure S2) developed using the *factoextra* (Kassambara & Mundt, 2020) and *ggbiplot* (Wickham, 2016) packages. Figure S1 was created and modified using Mapline (https://mapline.com). The data and script underlying this study are available as supplemental material.

3 | RESULTS AND DISCUSSION

3.1 | Location overview and genotype adaptability to the California region

The location, coordinates, weather, and management information are summarized in Table S1. For the samples in this experiment, the average yields ranged from 1996 kg ha^{-1} in Davis (2020–2021) to 6686 kg ha^{-1} in Davis (2017–2018), and GPC ranged from 7.9% in Imperial Valley (2020–2021) to 15.1% in Davis (2020–2021). Yolo region 3 was an

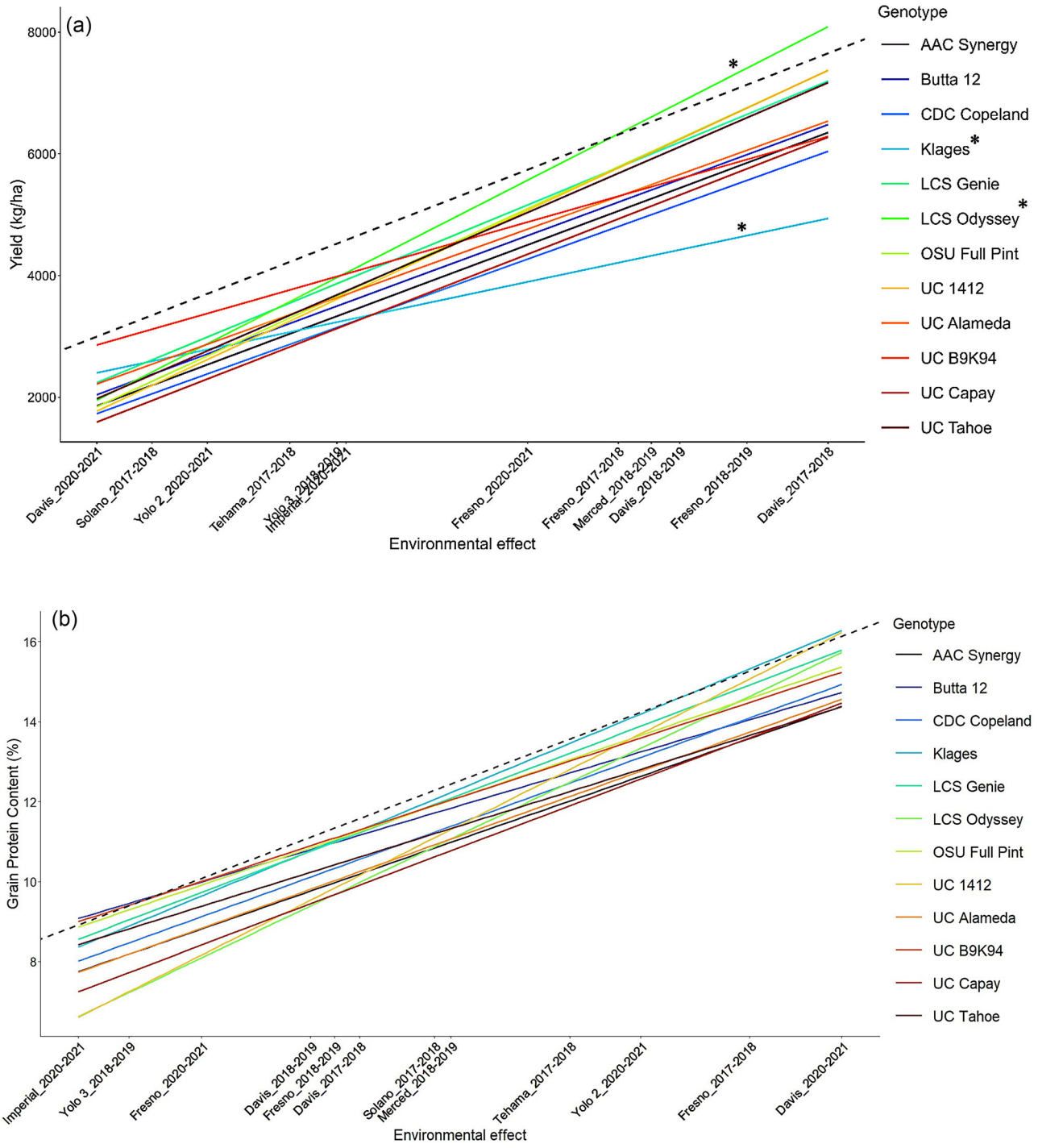

FIGURE 1 Finlay–Wilkinson regression of the 12 genotypes tested across eight locations and 3 years for adaptability of (a) yield (kg ha^{-1}); (b) grain protein content (GPC) (%). The *X*-axis denotes environmental effect (regression estimates for each location–year combination across all genotypes) and *Y*-axis denotes regression estimates for each genotype. Dotted line represents reference slope of 1. "*" represents a significant difference from reference slope (p-value < 0.05).

organically managed site with average yield and GPC of 3643 kg ha^{-1} and 8.4%, respectively (Table S3). The present study on malting barley included the 2020–2021 season, which was reported to be the warmest and driest season in the last century (California Department of Water Resources, 2021). Average values for productivity and grain quality traits summarized by genotype, location, and year are reported in Table S3.

Yield (kg ha^{-1}) and GPC (%) adaptability of these genotypes was assessed using FW regression (Figure 1; Finlay & Wilkinson, 1963). Adaptability (or responsiveness to a unit change in environmental index; hereafter "responsiveness")

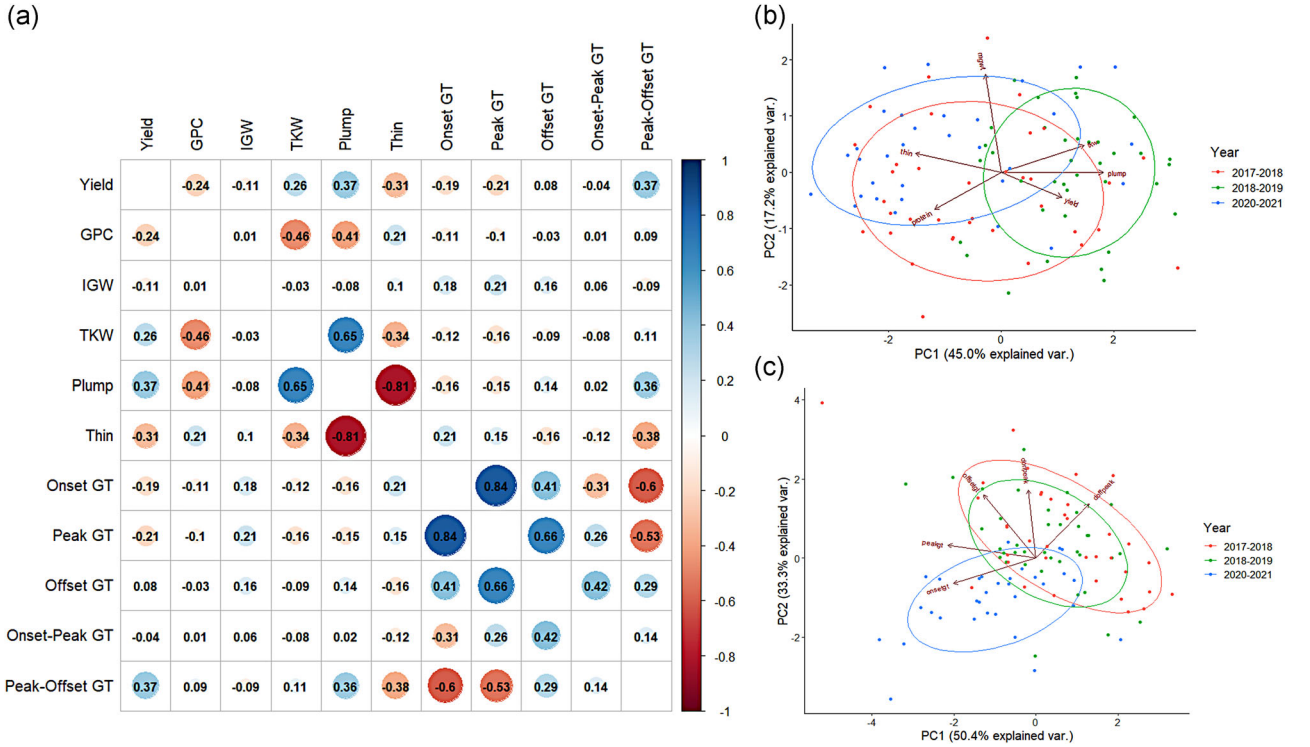

FIGURE 2 (a) Pearson correlation coefficient (*r*) matrix between malting barley productivity and quality traits. Colored circles indicate significant correlations based on a 95% asymptotic confidence interval using Fisher's *Z* transform; year based biplots for (b) productivity and quality traits principal components (PCs) 1 and 2; (c) gelatinization temperature (GT) traits PCs 1 and 2. Vectors represent yield (*yield*), grain protein content (GPC) (*protein*), percentage of plump (*plump*) and thin (*thin*) grains, individual-grain weight (*mgwt*), thousand kernel weight (*tkw*), onset GT (*onsetgt*), peak GT (*peakgt*), offset GT (*offsetgt*), difference between onset and peak GT (*donpeak*), and difference between peak and offset GT (*doffpeak*). Normal confidence ellipses based on multivariate *t*-distribution were drawn with 95% confidence intervals for all biplots.

was defined based on the slope of the regression line relative to the reference slope equal to one, with genotypes with higher responsiveness having slopes greater than one and genotypes with lower responsiveness having slopes less than one. All slope values and 95% confidence intervals for those values are reported in Table S2.

For yield (Figure 1a), LCS Odyssey (Limagrain Cereal Seeds, 2022) had higher responsiveness, and its slope was significantly different than one (slope = 1.37). Other genotypes with higher responsiveness (slopes greater than but not significantly different than one) were UC Tahoe (Hegarty et al., 2018), OSU Full Pint, and UC Alameda. Klages (Wesenberg et al., 1974) had low responsiveness with a slope of 0.69 that was significantly different than one. Other genotypes with relatively lower responsiveness (less than but not significantly different than one) were AAC Synergy (Legge et al., 2014), Butta 12 (Gallagher et al., 2020), and CDC Copeland (Canadian Food Inspection Agency, 2007). Klages, CDC Copeland, and AAC Synergy were developed in other production regions, whereas Butta 12 was developed for California. Some of these genotypes with relatively lower slopes and higher intercepts could have been developed for niche and/or low yielding environments. For example, Klages is not recommended for low rainfall regions or water-limited cropping, and AAC Synergy was specifically adapted for hot, humid summers in Western Canada (Legge et al., 2014). A minor trend of UC Tahoe slightly outperforming Butta 12 in irrigated environments (and vice versa in rainfed environments) was noted by Hegarty et al. (2018). The two lines appear to have diverged in higher yielding environments in this study as well (Figure 1), but with significant differences not detected in the present study (Table S2) nor in Hegarty et al. (2018).

For GPC (Figure 1b), the genotypes with highest responsiveness were Klages, LCS Odyssey, LCS Genie, and UC Capay (del Blanco et al., 2022). However, all genotypes were relatively responsive (or "adaptable") in GPC, and no slopes were significantly different than one. For the other traits analyzed in this study, certain genotypes that were observed in at least half of the environments in this study exhibited slopes significantly different than one (Table S2), which are the only slopes specified in the text. CDC Copeland had slope of 1.32 for TKW, and Butta 12, UC Capay, and UC Tahoe had slopes of 0.43, 0.54, and 0.56 (respectively) for TKW. UC Capay and LCS Odyssey had slopes of 0.42 and 1.60 (respectively) for onset GT, and LCS Odyssey had a slope of 3.07 for

TABLE 1 Percent variance explained by main and interaction effects of genotype (*G*), location (*L*), and year (*Y*) on traits of relevance to malting barley productivity and quality using linear mixed effects models.

Metric	Trait	*G*×*L*	*G*×*Y*	*L*×*Y*	*G*	*L*	*Y*	*G*×*L*×*Y*	*L*×*Y*×B	Res
Percent variance explained	Yield	0	0	44	4	11	8	11	5	16
	GPC	3	3	72	0	0	0	–	–	22
	TKW	2	8	21	33	0	26	–	–	10
	IGW	1	0	0	0	22	0	–	–	77
	Plump	0	10	4	18	0	30	–	–	38
	Thin	0	4	6	8	6	30	–	–	46

Note: "B" refers to block; "Res" refers to residuals.

Abbreviations: GPC, grain protein content; TKW, 1000-kernel weight; IGW, individual-grain weight.

difference between onset and peak GT. Finally, UC Capay had a slope of 0.51 for difference between peak and offset GT. No other slopes for genotypes tested in at least half of the environments in this study were significantly different than one, for any genotype–trait combination.

3.2 | Effects of *G*, *L*, *Y*, and their interactions on malting barley productivity and quality

The six productivity and grain quality traits in this study—yield (kg ha^{-1}), GPC (%), IGW (mg), TKW (g), and grain size (plump and thins)—were examined in an LME modeling framework. The percentages of variance explained by the main and interaction effects of *G*, *L*, and *Y* are shown in Table 1. For yield and GPC, the *L*×*Y* interaction accounted for 44% and 72% of the variance, respectively. The three-way interaction term *G*×*L*×*Y* accounted for 11% of the variance in yield. The largest variance for TKW was explained by *G* (33%), *Y* (26%), and *L*×*Y* (21%). The largest variance in plump was explained by *Y* (30%) and *G* (18%), and the largest variance for thins was explained by *Y* (30%). The linear model that was fit for IGW had a large extent of residual variance, potentially indicating that this trait is more dependent on specific management factors that were not explicitly tested in this model.

These results (Table 1) are in line with a previous genotype by environment study conducted in Ethiopia (Bantayehu, 2013), where location explained the largest variance in grain quality traits. Location and genotype effects significantly contributed to variance in GPC, which in turn was found to be a major driver of malt quality (Halstead et al., 2023). Interestingly, in studies where malt quality was assessed as opposed to grain quality (the latter was examined in the present study), the contribution of variance coming from *G* was larger than *L* and/or *Y* (Laidig et al., 2017; Nielsen & Munck, 2003). This highlights the need for a deeper understanding of how grain quality traits correlate with malt quality traits (e.g., total starch extract %, total β-glucan content). Furthermore, a more in-depth characterization of grain and malt quality parameters in a larger number of genotypes could also be worthwhile to inform selection in earlier stages of the breeding process. Enabling such characterizations at a greater scale and/or with higher throughput could have value to the industry and research community.

In mixed ANOVA for productivity and quality traits (Table S4), the terms exhibiting significance were generally concordant with the variance components results in Table 1. For yield, the *G*×*LY* interaction was significant, alongside main effects. In post hoc tests (Table S4), significant differences were detected for certain *G*×*LY* combinations. For example, LCS Odyssey (high) had significantly different means for yield than Klages (low) in Davis 2017–2018, Davis 2018–2019, and Merced 2018–2019. None of the four 2020–2021 environments were among the highest yielding environments for any genotype (Table S4), with a few exceptions (viz., Imperial 2020–2021 for LCS Genie and Fresno 2020–2021 for LCS Genie, CDC Copeland, and AAC Synergy). The Davis 2020–2021 environment consistently showed among the lowest means for all genotypes that were tested therein. The poor yields in that environment (and across locations in 2020–2021) were primarily due to drought and high temperatures. The Davis site is managed as a rainfed site with only minimal irrigation as needed (e.g., for successful establishment of the crop). Average daily maximum temperatures in the Davis 2020–2021 environment were 1.7˚C higher than the 10-year average between April 1 and May 31 (the period representing grain filling) (Nelsen, Merz, et al., 2021; PRISM Climate Group, 2020).

For protein, the *L*×*Y* interaction was significant alongside main effects. Notably, among the 2020–2021 environments, means for GPC from Davis and Yolo 2 (high) were significantly different than those from Fresno and Imperial (low), and the two sets of means varied by more than four percentage points for GPC (%). In this context, it is interesting to note again that no genotypes had slopes significantly different than one for GPC in FW regression. For IGW, the main

TABLE 2 Percent variance explained by main and interaction effects of genotype (*G*), location (*L*), and year (*Y*) on starch gelatinization temperature (GT) using linear mixed effects models.

Metric	Trait	*G*×*L*	*G*×*Y*	*L*×*Y*	*G*	*L*	*Y*	Res
Percent variance explained	Onset GT	6	9	12	23	1	26	24
	Peak GT	0	7	25	36	0	4	29
	Offset GT	2	5	30	23	0	0	39
	donpeak	7	9	1	0	6	7	70
	doffpeak	0	0	33	2	6	38	20

Note: Units are ˚C for all of the traits presented in this table. "Res" refers to residuals; "donpeak" refers to difference between onset and peak GT; "doffpeak" refers to difference between peak and offset GT.

effect of *L* was the only term that exhibited significance in mixed ANOVA, suggesting that continued monitoring of IGW in samples from regional trials would be helpful in the case of environmental and/or other effects that are not solely the main effect of genotype.

For TKW and plump, the *L*×*Y* interaction was significant, as were the main effects of each of *G*, *L*, and *Y* (Table S4). For both traits, two of the 2018–2019 environments (Davis and Fresno; high) had significantly different means than two of the 2020–2021 environments (Davis and Yolo 2; low). Butta 12 (high) had a significantly different mean for plump than all but two of the genotypes in this study; plumpness was indeed noted as one of the key favorable attributes of that variety at time of release (Gallagher et al., 2020). For thins, the main effects of *L* and *Y* were significant, and the 2020–2021 environments (high) had significantly different means than the other 2 years.

3.3 | Effects of *G*, *L*, *Y*, and their interactions on starch GT

The main and interaction effects of *G*, *L*, and *Y* on starch GT are shown in Table 2. For onset GT, the largest percentage of variance was explained by *Y* (26%), followed by *G* (23%). For peak and offset GT, the largest percentage of variance was explained by *G* (36% and 23%, respectively) and the *L*×*Y* interaction term (25% and 30%, respectively). In addition to onset, peak, and offset GT, it is also important to consider the GT temperature range using the difference between onset and peak GT and difference between peak and offset GT. A broader GT range will result in a wider DSC curve, which has been attributed to the presence of more A-type starch granules that have been packed heterogeneously (Suh et al., 2004; Vasanthan & Bhatty, 1996). Similar to IGW, the residual variance of the difference between onset and peak GT was large, suggesting that there could be variance associated with specific management factors that were not explicitly tested in this model.

The difference between peak and offset GT was substantially explained by *Y* (38%) and *L*×*Y* (33%; Table 2). It is possible that these effects were mediated by the amylose (A) to amylopectin (AP) ratio, and the percentages of small granules present in the grain. Amylose (A) and amylopectin (AP) ratios directly impact GT in malting barley, and it has been found that a higher A:AP ratio can trigger higher GT (e.g., higher peak and offset GT; Källman et al., 2015). It was previously reported that a higher A content (%) may cause it to entangle and/or co-crystallize with AP, thereby limiting starch swelling and subsequent hydrolysis (Tester & Morrison, 1990). This could result in an increased starch GT. Further examination of these trends in a wider sample set coming from varied *G*, *L*, and/or *Y* is needed for this assessment. High GTs have also been associated with an increased percentage of smaller starch granules in the barley endosperm (Langenaeken et al., 2019). These smaller starch granules are often developed due to changes in starch biosynthesis during grain development that are triggered by drought (Gous et al., 2015). Hence, a large extent of variance in the difference between peak and offset GT being explained by *Y* could prove to be problematic for the malting and brewing industries.

In mixed ANOVA for GT-related traits (Table S4), the terms exhibiting significance were generally concordant with the variance components results in Table 2. For onset GT and peak GT, the *L*×*Y* and *G*×*Y* interactions were significant alongside main effects. For onset GT, the 2020–2021 environments (high) had significantly different means than most of the other environments. For peak GT, the 2020–2021 environments again exhibited high means but with a less clear trend than that for onset GT. Although means for onset and peak GT were also significantly different between certain *G*:*Y* combinations, no clear trends were evident.

For offset GT, the *L*×*Y* interaction was significant, as were the main effects of *G* and *Y*. The Fresno 2018–2019 environment (high) had a significantly different mean for offset GT than all environments except for one (Tehama 2017–2018). LCS Odyssey and Butta 12 (high) had significantly different means for offset GT than UC Capay and OSU Full Pint (low); the remaining genotypes did not significantly differ from any of these four. For difference between offset and peak GT, the main effects of *G*, *L*, and *Y* were significant, with no significant interaction effects; Butta 12 (high) had a significantly different mean than LCS Odyssey (low). No terms were significant in mixed ANOVA for difference between onset and peak GT, such that post hoc tests were not conducted for that trait.

3.4 | Trait relationships (correlations and principal component analysis)

Pearson correlations were examined between the malting barley productivity and quality traits studied herein (Figure 2a).

Correlations discussed here are indicated using colored circles and were statistically significant based on a 95% asymptotic confidence interval using Fisher's Z transform. Yield was positively correlated with plump % ($r = 0.37$) and the difference between peak and offset GT (0.37) but was negatively correlated with thin % (−0.31) and peak GT (−0.21). GPC was negatively correlated with plump % (−0.41) and yield (−0.24). Peak GT was negatively correlated with yield (−0.21) and plump % (−0.15) but was positively correlated with IGW (0.21). TKW was positively correlated with yield (0.26) and plump % (0.65), but negatively correlated with GPC (−0.46) and thin % (−0.34). Interestingly, these traits were not significantly correlated with IGW except for thin % (0.1). The finding of TKW and plump % being among the strongest positively correlated traits ($r = 0.65$) suggests that measurements of TKW could be helpful to breeders and agronomists as an indirect assay for plump (e.g., if data for TKW is readily available for more genotypes and/or environments). In the range of TKW observed in the samples in this study (predominantly less than 47 g), TKW and plump showed a positive relationship in Vahamidis et al. (2022) (in the >2.5, 2.5–2.6, and >2.6 mm ranges for grain size). Vahamidis et al. (2022) also found plump to have higher plasticity than TKW (and yield) in two-row malting barley produced in Mediterranean climates, suggesting that TKW could be a less plastic proxy trait for use by breeders (and one that was also weakly positively correlated with yield in the present study)—with continued and routine monitoring of relationships between these traits.

The correlations between yield and GPC, and plump % and GPC, are generally accepted to be negative in malting barley (Fox, 2009; Vahamidis et al., 2022; Yu et al., 2017). However, newer studies have shown that potential explanations for this negative correlation could be due to nitrogen availability (Magliano et al., 2014) and/or tiller formation (Hu et al., 2021).

A few moderate-to-strong correlations were observed between GT traits (Figure 2a). Among these, the difference between peak and offset GT showed a positive correlation with yield (0.37) and plump % (0.36), negative correlation with thin % (−0.38), and strong negative correlation with onset GT (−0.60) and peak GT (−0.53). To date, the mechanism behind this extension of the gelatinization curve past the peak temperature has not been explained in the literature. We hypothesize that some alternative endosperm parameter not measured in this study could be underlying this extension. The positive correlation between plump and this difference trait could be attributed to the proportion of A- and B-type starch granules within the endosperm (Goering et al., 1973; Vasanthan & Bhatty, 1996). The smaller, B-type granules that are developed later in the grain filling process have been previously shown to gelatinize more slowly than A-type granules (Karlsson et al., 1983; Langenaeken et al., 2019). Hence, it is possible that the samples with a higher difference between the peak and offset GT assessed in this study could contain a higher proportion of B-type granules than A-type granules, indicated by the high plump (%). The negative correlation between onset GT and this difference trait could be due to variation in levels of hordeins (major seed storage proteins in the endosperm). Although the large starch granules gelatinize at relatively lower temperatures (indicated by onset GT), hordeins encompass the small starch granules and could impact their accessibility to starch-degrading enzymes (Wenwen et al., 2019). Further research on starch granule proportions and hordein content will enable a more comprehensive understanding of this complex relationship between starch GT and grain quality.

PCA biplots were used to visualize the relationships among traits across three years (Figure 2b,c). Normal confidence ellipses based on multivariate t-distribution were drawn with 95% confidence intervals for each year. For productivity and quality traits, the first, second, and third principal components (PCs) explained 45.0%, 17.2%, and 14.5% of the total variance, respectively. For the starch GT traits, the first and second PCs explained 50.4% and 33.3% of the total variance, respectively. The 2020–2021 season samples formed a partially distinct cluster, mainly discriminated by high percentage of thin grains (Figure 2b) and high onset GT (Figure 2c). These results are consistent with the results of post hoc tests for thins (for which the 2020–2021 environments had significantly different means than those from the other 2 years) and onset GT (for which the 2020–2021 environments had significantly different means than most of the other environments).

3.5 | Gelatinization profiles (differential scanning calorimetry curves)

Starch gelatinization curves for UC Tahoe and UC Capay were examined for each of the 3 years in this study (Figure 3). On average, onset GT was higher by approximately 1°C (but with a significant difference not detected) for the 2020–2021 season in comparison to other seasons for UC Tahoe (Table S4). The 2020–2021 season was characterized by a higher average maximum temperature during crop growth across the locations tested (Table S1). Moreover, a few sites in other seasons also experienced drought conditions (i.e., based on crop evapotranspiration in excess of soil water supply during the reproductive growth phase and accompanying observations of drought-related symptoms). Three out of four sites in the 2020–2021 season experienced terminal drought stress as also indicated by the water (precipitation and irrigation) levels post heading in Table S5. Hence, one possible explanation for higher onset GT for UC Tahoe (and in 2020–2021

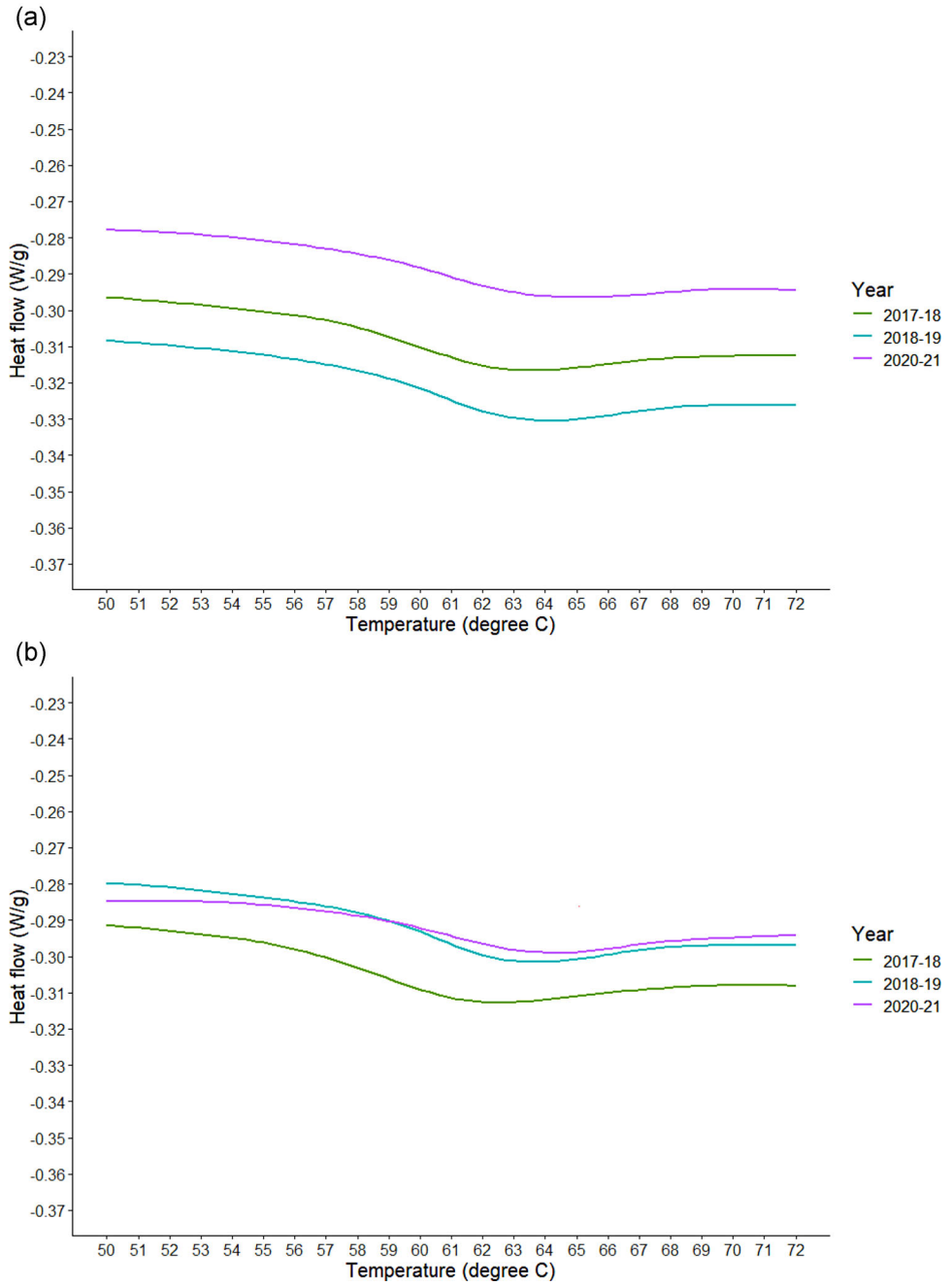

FIGURE 3 Average differential scanning calorimetry curves for (a) University of California (UC) Tahoe grown in 2017–2018 ($N = 4$ locations), 2018–2019 ($N = 4$) and 2020–2021 ($N = 3$); (b) UC Capay grown in 2017–2018 ($N = 4$), 2018–2019 ($N = 4$), and 2020–2021 ($N = 3$).

more generally, as appeared in the PCA results; Figure 2c) is that the extreme weather conditions during grain-fill could have led to the formation of smaller (i.e., a higher percentage of B-type) starch granules within the endosperm, which subsequently could have led to higher onset and peak GTs (Tables S3 and S4). Colder summer temperatures have been shown to lower the peak GT in a barley study in Finland (Myllärinen et al., 1998) compared to climate-typical summers, which is further indicative of a positive relationship between starch GT and growing season temperature.

4 | CONCLUSION

This study was the first assessment of the combined effects of *G*, *L*, and *Y* on starch gelatinization. It was also the first study to assess malting barley productivity and grain quality for the Californian region, while providing information regarding the adaptability of genotypes grown in this region for these traits. The largest variance in yield, GPC, plump and thin grains, and IGW were explained by either *L*, *Y*, or their interaction. Variance in TKW, on the other hand, was

largely explained by *G* and *Y*. We also confirmed that *Y* and the *L* × *Y* interaction term explained the largest variance in onset and offset starch GT, respectively, but the largest variance in peak GT was explained by *G*. Finally, the 2020–2021 season formed partially distinct clusters in PCA, segregated by a high percentage of thin grains and high onset GT. These findings illustrate the critical role of *G*, *L*, and *Y* in determining malting barley productivity and grain quality in California.

AUTHOR CONTRIBUTIONS

Maany Ramanan: Conceptualization; data curation; formal analysis; investigation; validation; visualization; writing—original draft. **Taylor Nelsen**: Resources; visualization; writing—review and editing. **Mark Lundy**: Investigation; resources; writing—review and editing. **Glen Patrick Fox**: Conceptualization; funding acquisition; supervision; writing—review and editing. **Christine Diepenbrock**: Conceptualization; formal analysis; funding acquisition; resources; supervision; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors report no conflicts of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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