Received: 23 September 2020 | Accepted: 4 January 2021

DOI: 10.1002/csc2.20459

Crop Science

ORIGINAL RESEARCH ARTICLE

Crop Breeding & Genetics

Specific adaptation for early maturity and height stability in Icelandic spring barley

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Assigned to Associate Editor Steve Larson.

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Abstract

Cereal production in important growing regions is negatively influenced by climate change. This can be countered by expanding cereal production northwards in Scandinavia and Iceland, where today, barley (*Hordeum vulgare* L.) is primarily used as feed, as it rarely reaches malting quality. This study explores genetic factors underlying the ability of barley to mature fully in low temperature and long photoperiod. A panel of 84 spring barley lines were grown in controlled environments with different day lengths and temperatures, partially mimicking the target environment. The panel was screened for accumulated heat sum to heading, maturity, and height, all traits of importance for adaptation to the northern periphery. Subgroups with different stability and heat sum requirements were found, and day-length-neutral lines were identified. Height was temperature controlled, with lower temperature resulting in taller plants. The results were coupled to a genome-wide association study (GWAS). Despite the small panel size, the *Mat-a* locus was identified to have the strongest association with heat sum to heading; *Ppd-H1*, *Mat-a, FT1*, and *DHAR2* with heat sum to maturity; and *GA20ox1* with height. Early maturing lines with height stability have successfully been developed in Iceland, and this study confirms their performance in controlled environments for the first time. It provides insight to the mechanisms behind early maturity that will increase our ability to further adapt barley and other cereals to the northern climate. This will facilitate breeding work toward combining early maturity and height stability with traits such as quality, further enabling the northward expansion of grain production.

1 | INTRODUCTION

Barley (*Hordeum vulgare* L.) is the most widely adapted of the cereals (Ullrich, 2011) and, as such, is better suited to many marginal areas than, for example, wheat (*Triticum aestivum* L.). The environmental adaptation makes it the most important cereal crop in high latitude regions such as northern Scandinavia and Iceland (Nuttonson, 1957; Peltonen-Sainio

Abbreviations: BLUE, best linear unbiased estimate; GA, gibberellic acid; GDD, growing degree-days; GLM, general linear model; GWAS, genome-wide association study; HD, days to heading; HSHD, heat sum to heading; HSMD, heat sum to maturity; LDC, long day cold; LDW, long day warm; MD, days to maturity; MLM, mixed linear model; MLMM, multilocus mixed linear model; MTA, marker–trait association; NIL, near-isogenic line; PCA, principal component analysis; QQ, quantile–quantile; QTL, quantitative trait loci; SDC, short day cold; SDW, short day warm; SNP, single nucleotide polymorphism.

et al., 2011). Despite its adaptability, grain yield in the more northern regions still trails behind more favorable areas, with the average barley yield in Norway, for example, at 4.2 t ha^{-1} in 2017 vs. yields in regions such as Denmark and Germany with 6.0 and 6.9 t ha^{-1}, respectively (http://faostat.fao.org). Reports show stagnating yields in southern and central Europe (Schils et al., 2018), while yields in northern Europe are still rising (Moore & Lobell, 2015). Dawson et al. (2015) attribute this to effects of climate change, with the prediction that the impact will be even stronger in the future. Breeding of cultivars better adapted to local environments could potentially close the yield gap in northern latitudes. Research by a joint Nordic consortium for the promotion of plant breeding (Samnordisk planteforædling, 1992) showed that temperature is the climatic factor that mostly affects plant growth in northern Scandinavia. Iceland is at the margin of possible barley cultivation with a low temperature and a long photoperiod, the warmest month of the year averages 11 ˚C (Icelandic Meteorological Office). The growing season is relatively long in Iceland with sowing usually possible in the latter half of April and harvest in September (Hilmarsson et al., 2017). However, because of its maritime climate, the accumulated heat sum during the growing season is lower in Iceland than other regions at comparable latitudes (Martin et al., 2017) especially during the grain-filling period in late summer and early fall. The effects of climate change are particularly difficult to predict in Iceland where models range from an increase to even a slight reduction in temperature caused by the melting of Greenland ice cooling the ocean around Iceland (IPCC, 2018). One unambiguous effect of climate change is more extreme weather events (Trnka et al., 2014). Tall plants are prone to lodging after strong winds accompanied by heavy rainfall, thus leading to yield losses (Dockter & Hansson, 2015). The ability to withstand strong winds, occasionally in combination with heavy rainfall, is a crucial character for a stable yield in Iceland (Bragason, 1985). Experience from 40 yr of barley breeding and cultivar testing in Iceland (e.g. Hilmarsson et al., 2017) has pinpointed the most limiting factor in the northernmost areas of barley cultivation to be the ability to reach maturity in low temperature. The flowering time is also important, as a plant flowering too early may risk damage during anthesis because of late spring frosts, whereas flowering too late may risk that the crop does not fully mature before harvest (Bragason, 1985).

Genetic variation affecting the photoperiod response has enabled the successful expansion of barley cultivation from its origin in the Fertile Crescent to northern latitudes (Jones et al., 2008; Turner et al., 2005). Based on their response to altered day lengths, plants can be divided into three types: long-day responsive plants that flower in the spring under increasing day lengths, short-day plants that initiate flowering in response to shortening of the day in autumn, and day-length-neutral plants that flower irrespective of day length and take their cues from temperature (Andrés & Coupland, 2012).

Core Ideas

- Early maturity and height stability are key traits in adaptation of cereals to high latitudes.
- We investigated effect of day length and temperature on a panel of Nordic spring barley.
- Temperature had effect on plant height with few lines showing height stability.
- Heat sum requirement to maturity varied among the panel according to day length.
- Key MTAs found in a GWAS included *GA20ox1*, *Mat-a*, *Ppd-H1*, and *FT1*.

The progenitor of cultivated barley is a long-day responsive plant that flowers when day length exceeds a critical length but shows a substantial delay in flowering when grown under short-day conditions (Laurie et al., 1995), although, day-length-neutral plants have also been identified and genetically characterized (Gustafsson et al., 1971; Milec et al., 2013; Zakhrabekova et al., 2012). In northern latitudes (>60˚ N), spring sown barley is the predominant cereal crop, and it has been characterized by a photoperiod nonresponsive allele in the *Ppd-H1* locus delaying flowering in spring-sown barley plants to utilize the season with increased day length for vegetative growth, thereby increasing total yield (Sharma et al., 2020; Turner et al., 2005). A mutation in the *Mat-a* (synonyms *Eam8*; *ELF3*) gene has been attributed to enabling barley cultivation in northern Scandinavia and Iceland (Zakhrabekova et al., 2012). Spring barley plants carrying the mutated *mat-a* allele flowers earlier in long-day conditions (Faure et al., 2012; Zakhrabekova et al., 2012).

Plant height is an important trait in barley adaptation to windy and rainy environments since short and strong stems help to prevent lodging in addition to positively affecting the harvest index (Hay, 1995). Allelic variants of semidwarfing genes have been widely employed in modern barley breeding (Kuczyńska et al., 2013; Wang et al., 2014). Modern European barley cultivars generally depend on allelic variation in the *denso/sdw1* locus as their source of semidwarfing (Kuczyńska et al., 2013). Previously, it has been reported that the gibberellic acid (GA) responsive locus *denso/sdw1* influences both height and earliness in barley (e.g. Göransson et al., 2019; Jia et al., 2009).

Icelandic barley cultivars have shown extreme earliness in multilocation field trials from Bavaria (Germany) in the south to Iceland in the north, suggesting that lines selected in the low temperatures in Iceland have a lower heat sum requirement to heading and maturity (Göransson et al., 2019). Another observation from field trials is that many barley cultivars grow taller in Iceland than in other North European regions, such as Scandinavia, giving rise to speculation that the low temperature may affect the height of the plant (Göransson et al., 2019).

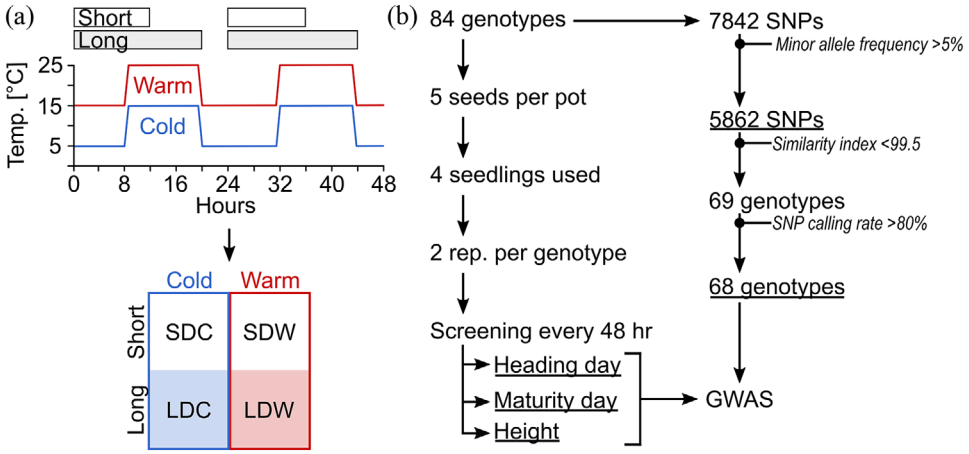

FIGURE 1 Experimental setup and overview of analysis. (a) Plants were kept at two day lengths, long day (20 h light/4 h dark) and short day (12 h light/12 h dark), each at two different temperature settings, cold (5–10 ˚C for 12 h, 15 ˚C for 12 h), and warm (15 ˚C for 12 h, 25 ˚C for 12 h), resulting in four different treatments: long day cold (LDC), long day warm (LDW), short day cold (SDC), and short day warm (SDW). (b) Eighty-four genotypes were selected for analysis and screened for three phenotypes: heat sum to heading, heat sum to maturity, and height. Each genotype was initially screened for 7,842 single nucleotide polymorphisms (SNPs) reduced to 5,862 SNP; after quality control the number of genotypes was reduced from 84 to 68 (see text for details)

The objectives of the current study are (a) to study effects of day length and temperature on the traits heat sum to heading, heat sum to maturity, and plant height on a panel of barley lines from Iceland and Scandinavia, and (b) to determine the quantitative trait loci (QTL) affecting the phenotypic differences.

2 | MATERIALS AND METHODS

2.1 | Plant material, growth conditions, and phenotyping

Twenty-seven two-rowed and 57 six-rowed spring barley cultivars and breeding lines of northern European origin were selected for analysis (Table 1). The lines were selected with the aim of representing diversity in heat sum requirements to maturity and day-length responses. The selection was based on previous results from performance in field trials (Nurminiemi et al., 1996), experience from the Icelandic barley breeding program (J. Hermansson and M. Göransson, unpublished results) and the results of a preliminary greenhouse study (M. Lillemo, unpublished results). Three near-isogenic lines (NILs) with allelic diversity at the *Mat-a* and *Uzu* loci were included along with their two-rowed mother cultivar Bowman to compare the phenotypes of known mutant lines with the Nordic population.

Seeds were sourced from (a) the original collection used by Nurminiemi et al. (1996) (these accessions were regenerated in greenhouse conditions prior to the experiment and later deposited at the regional gene bank, NordGen [www.nordgen.org]), (b) newly regenerated seeds from the Icelandic barley breeding program (Agricultural University of Iceland), (c) from the Byggbasis collection at Norwegian University of Life Sciences (regenerated in greenhouse prior to the experiment), and (d) 12 accessions were sourced from NordGen (Table 1). Five seeds per line were sown in 2-L pots with potting mixture (peat soil with clay and sand, Gartnerjord, Tjerbo, Norway). After emergence, four seedlings (or less if the germination was poor) were kept. No large deviations in plant emergence were observed except for two pots where no seeds germinated, and these are marked as 'NA' in the data set (Supplemental Table S1). The experiment had two replicates in each treatment, giving 168 pots in each of the four climate-controlled greenhouse chambers. The lines were grown for 180 d in four different environments in a climate-controlled greenhouse (Figure 1). The contrasting temperatures were chosen to approximately span the variation in growing season temperature for barley in the Nordic region in current and future climate (Børgesen & Olesen, 2011; Hilmarsson et al. 2017). The contrasting photoperiods of 20 and 12 h were chosen to enable detection of day-length responses (Kikuchi et al., 2012; Zakhrabekova et al., 2012). The treatments were (a) long day cold (LDC) with 20 h of light (illumination with high-pressure sodium lamps) and a recorded average temperature of 10 ˚C (~15/5 ˚C [day/night, each temperature period lasting 12 h]), (b) long day warm (LDW) with 20 h of light and a recorded temperature of 19.7 ˚C (~25/15 ˚C), (c) short day cold (SDC) with 12 h of light and a recorded temperature of 13.1 ˚C (~15/10 ˚C), and (d) short day warm (SDW) with 12 h of light and a recorded temperature of 19.9 ˚C (~25/15 ˚C). Temperature and humidity (maintained at constant 60%) were recorded continuously to monitor if the selected parameters were maintained

TABLE 1 Barley lines used in the experiment

Entry	Name	Row type	Seed source[a]	Accession number	Origin	Pedigree[b]	Release year[b]
1	'Brage'	6	Byggbasis	–	Norway	Lavrans//NK91650	2010
2	'Heder'	6	Byggbasis	–	Norway	SWN93162/Fager	2007
3	'Tiril'	6	Byggbasis	–	Norway	VoH91723/Arve	2004
4	'Edel'	6	Byggbasis	–	Norway	Tore/Verner	2002
5	'Helium'	2	Byggbasis	–	Denmark	Meltan/Delibes	2001
6	'Iver'	2	Byggbasis	–	Norway	Tyra/P-13	2001
7	'Marigold'	2	Byggbasis	–	France	UN97-5/UN1750	2009
8	'Iron'	2	Byggbasis	–	Denmark	Marnie/LP 813.6.98	2011
9	'Tyra'	2	Byggbasis	–	Norway	Sold/3/Birgitta/Mari//Gunilla	1988
10	'Trine'	6	SLU	NGB 6604	Norway	Lise × Clermont	1986
11	H3003	2	NordGen	NGB24716	Norway	Vada/203-7489//Jessica	–
12	'Lise'	6	Byggbasis	–	Norway	Asplund/DS295//Varde	1964
13	'Tunga'	6	SLU	NGB25777	Norway	Fræg//Juli/Rigel	1975
14	'Triumph'	2	SLU	NGB31409	Germany	Alsa/S 3170//11719-5913/Union/4/Diamant	1973
15	'Lavrans'	6	Byggbasis	–	Norway	Vera//Arve/H82009-1-3	1999
16	'Arve'	6	Byggbasis	–	Norway	Otra/Vigdis//Agneta	1990
17	HJA71384	6	SLU	NGB25765	Finland	Hankkija-673/Pomo	–
18	HJA77028	6	SLU	NGB24647	Finland	Eero mutant	–
19	Sigur_F	6	SLU	NGB25766	Faroe Islands	Landrace	–
20	'Tampar'	6	NMBU	NGB25785	Faroe Islands	Landrace	–
21	Is_046	2	SLU	NGB24648	Iceland	Mari/Tampar//Akka/Sigur-F	–
22	Vo_H_10660	6	SLU	NGB24651	Norway	Otra/Vigdis//Agneta	–
23	'Bode'	6	SLU	NGB25784	Norway	Pirkka/Nordlys	1978
24	'Fraeg'	6	SLU	NGB25783	Norway	Asplund/Maskin	1948
25	IGP_Fg_672_2_10_1	6	SLU	NGB25782	Norway	Fraeg mutant	1964
26	IGP_M_268	6	SLU	NGB25781	Norway	Fg-672-2-10-1/Dc-y-69b	1968
27	'Varde'	6	SLU	NGB25779	Norway	Asplund/Maskin	1941
28	'Yrjar'	6	SLU	NGB25778	Norway	Jarle/Varde	1975
29	HJA78045	6	SLU	NGB24657	Finland	Eero/Pomo//Potra	–
30	'Agneta'	6	SLU	NGB31405	Sweden	Asa/Frisia//Monte Cristo/4 x Edda II	1978
31	'Bamse'	6	SLU	NGB25775	Norway	2 x /IAsa/Frisial3/Monte Cristo/4 x Edda II	1981
32	'Jo_Silja'	6	SLU	NGB25774	Finland	Seger/Vega (6r)//Suvi	1979
33	'Arla'	2	SLU	NGB25770	Sweden	Maja/3/Hanna/Svanhals//Opal/4/Tammi	1962
34	'Akka'	2	SLU	NGB25769	Sweden	Monte Cristo/6 x Arla	1970
35	IPK_H2207	6	SLU	NGB24666	Norway	Lise/Paavo//Agneta	–
36	VoH2845	6	SLU	NGB24669	Norway	Bamse/4/Otra/3/Anital/Bonus/Varde	–
37	HJA78023	6	SLU	NGB24676	Finland	Olli/Hiproly//Kajsa	–
38	IGP_58	6	SLU	NGB25793	Norway	Domen/Fraeg	1968
39	IGP_H349220	6	SLU	NGB24677	Norway	Bode/Agneta	–
40	VoH2825	6	NordGen	NGB24681	Norway	Bamse/Yrjar	–
41	JO_1279	6	SLU	NGB25796	Finland	Otra/Etu	–
42	IGP_H349_10	6	NordGen	NGB24697	Norway	Bode/Agneta	–
43	HJA77061_Eero80	6	SLU	NGB25797	Finland	Olli/Eero	1985

(Continues)

TABLE 1 (Continued)

Entry	Name	Row type	Seed source[a]	Accession number	Origin	Pedigree[b]	Release year[b]
44	JO_1252	6	SLU	NGB24708	Finland	Varde/Otra	–
45	JO_1328	6	SLU	NGB24711	Finland	Suvi/Otra	–
46	HJA_77065	6	SLU	NGB24718	Finland	Etu/Pirkka	–
47	JO_1103	6	SLU	NGB25803	Finland	Varde//Opal/Perttu	–
48	JO_1310	6	NordGen	NGB24725	Finland	Jet/Ingrid	–
49	JO_1297	6	SLU	NGB24736	Finland	Suvi/Pirkka	–
50	JO_1184_Arra	6	SLU	NGB25808	Finland	Varde/Otra	1982
51	JO_1343	6	SLU	NGB24756	Finland	Varde/Otra	–
52	'Nairn'	2	AUI	–	Scotland	TRUMPF/HB-855-467-8	1984
53	Scots_Bere	6	AUI	–	Scotland	Landrace	–
54	247_1	6	AUI	–	Iceland	Arve/Hrutur	–
55	247_11	6	AUI	–	Iceland	Arve/Hrutur	–
56	Hrutur	6	AUI	–	Iceland	Arve//Nairn/VoH2825	–
57	'Kria'	2	AUI	NGB 16564	Iceland	Pernilla/Skegla	2004
58	'Skegla'	2	AUI	NGB 16565	Iceland	Pernilla/VoH2825//Pernilla	2002
59	291_13	6	AUI	–	Iceland	Arve/Skumur III	–
60	291_8	6	AUI	–	Iceland	Arve/Skumur III	–
61	294_12	6	AUI	–	Iceland	Arve/SjD918011//TIRIL	–
62	'Skumur_III'	6	AUI	–	Iceland	ARVE/SjD918011	–
63	SjD918011	2	AUI	–	Denmark	046/JO1328//Sepac	–
64	'Golf'	2	SLU	NGB25795	UK	Armelle/Lud//Luke	1983
65	'Pernilla'	2	SLU	NGB25768	Sweden	Birgitta/Mari//Gunilla	–
66	'Mari'	2	AUI	–	Sweden	Bonus mutant	1960
67	'Asa'	6	AUI	NGB 1487	Sweden	Dore/Wega	1949
68	'Asplund'	6	Byggbasis	–	Sweden	Selection from a mix of Primus I and 6-row barley	1910
69	'Maskin'	6	Byggbasis	–	Norway	Line selection from the landrace Bjorneby	1918
70	'Gunilla'	2	Byggbasis	–	Sweden	Birgitta x Opal/Vega//Gull mutant 44-3	1973
71	'Skumur_I'	6	AUI	–	Iceland	ARVE/SjD918011	–
72	'Teista_II'	2	AUI	–	Iceland	Sunnita/2//Akka/046	–
73	HJA_Hankkija673	6	SLU	NGB25807	Finland	Otra/Paavo	1973
74	JO_1315	6	NordGen	NGB24688	Finland	Tammi mutant	–
75	'Elmeri'	6	Byggbasis	–	Finland	–	2009
76	'Sepac'	2	AUI	–	Denmark	SEWA/PF-52296	1990
77	'Amalika'	2	AUI	–	Denmark	–	–
78	'Morex'	6	NordGen	NGB 23015	USA	Cree/Bonanza	1978
79	'Mona'	2	NordGen	NGB 1499	Sweden	(Mildew resistant line of Mari) × Monte Cristo	1970
80	'Barke'	2	NordGen	NGB 16758	Germany	Libelle/Alexis	1996
81	'Bowman'	2	NordGen	NGB 22812	USA	Klages//Fergus/Nordi /3/ND1156/4/Hector	1984
82	Bowman_NIL_Eam8_w	2	NordGen	NGB20574	USA	Bowman mutant	–
83	Bowman_NIL_Erectoides_o_16	2	NordGen	NGB 22114	USA	Bowman mutant	–
84	Bowman_NIL_Uzu1	2	NordGen	NGB20787	USA	Bowman mutant	–

[a]Seeds were sourced from (1) the original collection used by Nurminiemi et al. (1996) stored at the Swedish University of Agricultural Sciences (SLU), (2) newly regenerated seeds from the Icelandic barley breeding program at the Agricultural University of Iceland (AUI), and (3) from the Byggbasis collection at Norwegian University of Life Sciences, and (4) NordGen.

[b]References for the pedigree data and release year were Nurminiemi et al. (1996), NordGen database (www.nordgen.org/sesto), and information from breeders and breeding companies.

(Supplemental Figure S1). The short-day treatment was secured by automated mechanical covering of the plants with dark curtains to effectively provide darkness during night, as the greenhouse chambers could otherwise have been exposed to daylight or light from neighboring chambers with lamps. The actual temperature in each climate-controlled greenhouse chamber throughout the experiment was used in subsequent heat sum calculations.

Plants were supported with bamboo sticks and tied up to prevent falling over and were continuously watered on a daily basis to avoid any drought stress. The pots were fertilized one to two times per week using a 1.2 mg L^{-1} nutrient solution consisting of a 1:1 mixture of calcium nitrate and Yara Kristalon (9–11–30, 7 MgO + micro) from the two-leaf stage until the first spikes matured. All plants were treated twice during the grain-filling stage with 1.25 ml L^{-1} Forbel 750 (fenpropimorph, BASF) and 350 mg L^{-1} Confidor 70 WG (imidacloprid, Bayer) to prevent powdery mildew infections and thrips. In addition, a preventive treatment with a sulfur burner was maintained throughout the experiment to prevent mildew infections. The plants were screened every 48 h and the traits recorded were days to heading (HD), days to maturity (MD), height, and row type. Days to heading was registered as the day of ∼2 cm of awn emergence of the second earliest plant in each pot, corresponding to Zadoks growth stage 49 (Zadoks et al., 1974), which is the growth stage best corresponding to the actual fertilization event in spring barley (Alqudah & Schnurbusch, 2013). Days to maturity was recorded when the peduncle of the earliest straw of the second earliest plant in each pot turned yellow, indicating that the phloem ceased to allocate sugars to the kernels, corresponding approximately to Zadoks growth stage 87 (Zadoks et al., 1974). We chose to consistently report the heading and maturity of the second earliest plant in each pot. This was a precautionary measure to rule out bias from potentially mixed-in seeds (which we did not observe, all pots showed a consistent development). In the low-temperature treatments, the peduncle remained green in some cases after yellowing of the spike. For those cases, MD was scored when the kernels became mature (growth stage 87–89) (Zadoks et al., 1974). Days to heading and MD were used to subsequently calculate the accumulated heat sum (growing degree-days, GDD) for both HD and MD based on the recorded temperature in each climate-controlled greenhouse chamber, with a baseline temperature of 0 ˚C. The accumulated heat sum to heading (HSHD) and heat sum to maturity (HSMD) were used in subsequent analyses. Height, the third trait of interest, was recorded upon the closing of the experiment and was recorded as the height of the straw in centimeters from the soil level to below the spike as an average across all spikes in the pot. For plants that did not head, no straw length was registered. In cases where flowering had not occurred at the closing of the experiment, the apical meristem was dissected and inspected to record whether it remained in a juvenile stage or had initiated into a reproductive phase. In order to obtain quantitative data on all lines, the nonheading plants were assigned a heading day later than the closing of the experiments (180 d), and maturity 30 d later (210 d), considering that all the lines had entered the reproductive phase. The artificial heading and maturity days are marked in Supplemental Table S1. Row type was scored as two- or six-rowed spikes and was subsequently used to validate (a) that no mix-ups had been made during sowing and (b) that the data analysis worked, as peaks would be expected at the *Vrs1* and *Int-c* loci controlling the row type (Lundqvist et al., 1997) (Supplemental Table S6).

2.2 | DNA isolation and genotyping

Leaf tissue (∼50 mg fresh leaf) was sampled around growth stage 13 (Zadoks et al., 1974). The leaf tissue was homogenized using a Tissuelyser (Retsch) and DNA extracted using a standard protocol with the DNeasy extraction kit from Qiagen. Approximately 50 ng μl^{-1} of DNA from each sample were submitted to Trait Genetics, Germany, for genotyping using the 9K iSelect single nucleotide polymorphism (SNP) chip from Illumina (www.illumina.com), which contains 7,842 SNP markers (Comadran et al., 2012). A total of 5,862 markers were polymorphic at >5% minor allele frequency level and their physical positions (in base pairs) on the barley reference genome (Mascher et al., 2017) were retrieved using the online tool BARLEYMAP (Cantalapiedra et al., 2015). The similarity index was calculated using the function mcor (pairwise complete correlations) in R Studio (RStudio Team, 2020), with a threshold of 0.99. Fifteen lines had a similarity index >99.5 with one or more lines and were thus excluded from genetic analyses (Supplemental Table S2). These lines were still included in phenotypic data as their relatedness could in many cases be explained by their recent pedigree. One line had a SNP calling rate <80% and was excluded from genetic data analyses. Thus, in all, 68 lines remained in the genetic data analyses (Figure 1b).

2.3 | Data analysis

The traits showed a normal distribution, and Pearson correlations between traits and environments were calculated using package corrplot (Wei & Simko, 2017) in R Studio (RStudio Team, 2020). Analysis of variance was calculated on randomized complete blocks using META-R v. 6.0 (Alvarado et al., 2016).

The model $Y_{ijk} = \mu + \mathrm{Env}_i + \mathrm{Rep}_j\left(\mathrm{Env}_i\right) + \mathrm{Gen}_k + \mathrm{Env}_i \times \mathrm{Gen}_k + \varepsilon_{ijjk}$ was used.

where Y_{ijk} is the trait of interest, μ is the overall mean effect, Rep_j is the effect of the jth replicate within the ith environment, Gen_k is the effect of the kth genotype, $\text{Env}_i \times \text{Gen}_k$ is the effect of the environment × genotype interaction, and ε_{ijjk} is the effect of the error associated with the ith environment, jth replication, and kth genotype. Environment and genotype were considered to be fixed effects and the best linear unbiased estimates (BLUEs) were analyzed as values of the two replications in each environment. Fisher's test was used to calculate differences between the treatments and genotypes (Minitab 17 Statistical Software, 2010). Broad-sense heritability for the traits in each respective treatment was calculated using META-R v. 6.0 (Alvarado et al., 2016). A population structure within a given set of barley genotypes can cause false positives in associations between markers and traits. The software STRUCTURE v. 2.3.4 (Pritchard et al., 2000) was used to predict the most likely number of subpopulations (K), with Markov chain Monte Carlo set to 9,999 burn-in phases and 9,999 iterations run 10 times for each simulated number of K between 1 and 12. Structure Harvester v.0.6.94 (Earl & von Holdt, 2012) was used to determine the most likely K using the method of Evanno et al. (2005). Principal component analysis (PCA) was performed using the genotype data to further explore population structure. To find marker–trait associations (MTAs) a genome-wide association study (GWAS) was performed using the R-package Genome Association and Prediction Integrated Tool (GAPIT v.3.0) (Lipka et al., 2012) following the methods in Göransson et al. (2019). Kinship matrices were constructed following the van Raden method incorporated in GAPIT. In subsequent mixed linear model (MLM) analyses (Yu et al., 2006; Zhang et al., 2010) the kinship matrix, K-values, and PCA eigenvalues were used to account for population structure. To select the optimal model, four single-locus and one multilocus models were tested: (a) general linear model (GLM) without a population structure, (b) MLM using van Raden kinship, (c) MLM using van Raden kinship and Q-values from the STRUCTURE analysis, (d) MLM with van Raden kinship and eigenvalues from the PCA, and (e) multilocus mixed linear model (MLMM) using van Raden kinship. Quantile–quantile (QQ) plots were constructed by comparing expected and observed $-\log(p)$ values (Supplemental Figure S2). Models were evaluated based on the QQ plots (large deviations from the expected distribution mean that the model does not fit the data) to select the most appropriate model for the population. Bayesian information criterion values were zero for eigenvalues from the PCA and hence these were excluded from the model evaluation. Out of the tested models and for all traits except spike morphology (two- vs. six-rowed phenotypes), the MLMM gave the strongest associations and was best in terms of correcting for both false positives and false negatives. For row type, the best model was MLM using van Raden kinship and Q-values. The MLMM is generally better suited to handle quantitative traits controlled by many loci in structured populations (Segura et al., 2012). Thus, for subsequent analysis, MLMM was used for HSHD, HSMD, and height. Manhattan plots showing positions of associated markers across the genome were constructed for each trait based on the MLMM results using the R package CMplot (Yin et al., 2020). Genome-wide association study was performed for each environment and trait based on the calculated BLUEs. A cut-off value of $-\log(p) \geq 3$ was used as the significance level for the association analysis (Li et al., 2012). Zhang et al. (2019) have recently recommended this cut off in multilocus GWAS to balance between the high power and low false positive rate for MTAs. For allele effects across the environments output from the MLM was used, whereas allele effects for specific environments were calculated based on the BLUEs for the respective environment. The interval lengths of the QTL were decided by calculating the linkage disequilibrium between the most significant markers at each intra-chromosomal locus using TASSEL v. 5.2.31 (Bradbury et al., 2007) and evaluating the linkage disequilibrium plot based on r^2 value and D prime, with threshold values of approximately 0.7 and 0.8, respectively. Barleymap (Cantalapiedra et al., 2015) and Barlex (Colmsee et al., 2015) was used to search for putative loci near the significant MTAs, with an approximate search window of <5 Mpb from the SNP marker. Allele combinations for MTAs with previously known earliness loci were tested for significance between groups (confidence interval 0.95) using ANOVA and Tukey's test, using the RStudio (RStudio Team, 2020) packages emmeans (Lenth, 2020), multcomp (Hothorn et al., 2008), and boxplots were constructed using the package ggplot2 (Wickham, 2016). Stability plots obtained from the genotype × environment analysis with R (GEA-R) v.4.1 (Pacheco et al., 2016) software were used to visualize the CV plotted against the BLUEs across environments trait wise for each genotype. The model used randomized complete blocks run as a linear regression model. All environments were included in the stability models for HSHD and HSMD, whereas for height the SDW environment was excluded because of missing data for the trait. A phenotype stable under different environments will lead to a lower CV value, while a higher CV suggests a stronger environmental effect in one or more environments. Figures 1 and 7 were created using Inkscape (https://inkscape.org).

3 | RESULTS

3.1 | ANOVA

The ANOVA showed the environment to be of largest effect in all traits (Supplemental Table S4). For HSHD and HSMD, the environmental effect accounted for >60% of the variation, whereas for height, there was only a small difference in

effect between the environment and the genotype effect (45 and 44% of the total variation, respectively). For all traits, the genotype × environment interaction was smallest (but significant for all traits). The data from all four environments were significantly positively correlated among each trait, the range of r values were 0.55–0.82, 0.24–0.65, and 0.4–0.86 for HSHD, HSMD, and height, respectively (Supplemental Figure S3). All four treatments had significant correlations between HSHD and HSMD (range of r values 0.32–0.94), whereas height was poorly or not correlated with HSHD and HSMD.

3.2 | Earliness

The heat sum requirement to heading showed a clear variation in plant phenotypes affected by the environments, ranging from long-day-responsive lines, which headed earlier in long-day conditions to lines with day-length neutrality that headed irrespective of day length (Figure 4). The broad-sense heritability (H^2) for HSHD were 0.87, 0.90, 0.80, and 0.80 for LDC, LDW, SDC, and SDW, respectively (Supplemental Table S3). Eleven lines, including both row types, proved to be day-length neutral for HSHD (Figure 2), two of these were NILs of cultivar Bowman with known mutations at the *Mat-a* locus (Bowman NIL Eam8.w and Bowman NIL Erectoides o.16). The other nine were cultivar Mari and eight other Nordic spring barley lines ('Teista II', IS-046, HJA77061(Eero80), 'Tyra', 'Iver', 'Mona', H3003, and HJA77028) all of, which have Mari in their pedigrees. Six lines did not reach the heading stage in SDW (Figure 2), with a dissection at the closing of the experiment showing that all of them had altered the meristem into the reproductive stage but had stagnated and not proceeded to bolting. This was seen in the Swedish cultivar Asplund and five others, which all had Asplund in their pedigrees. When the two long-day environments were compared, the HSHD was consistently higher in LDW than in LDC (Supplemental Figure S4). A stability plot of the phenotype data (Figure 3a) revealed a grouping of the day-length-neutral lines in the lower left corner. The lines that did not head in SDW grouped in the top right corner. A group of early stable lines grouped in the lower left square above the red marked lines (line 55, 247_11; line 58, 'Skegla'; line 57, 'Kria'; line 54, 247_1; line 56, Hrutur; and line 71, 'Skumur I') where all were selected in Iceland, except for one line from the Faroe Islands (line 20, Tampar) and one line from Finland (line 37, HJA78023).

Heat sum to maturity largely followed the pattern of the HSHD (Figure 2), meaning that HSMD was relatively constant irrespective of ambient temperature. However, there was a significant difference between the two long-day treatments ($p = .0068$), where a subgroup of primarily Icelandic lines showed a contrasting heat sum requirement from most other lines; instead of requiring a lower accumulated heat sum in LDC (as most lines) they required a higher heat sum in LDC (Supplemental Figure S4). Broad-sense heritability for HSMD was 0.70 in LDC, 0.90 in LDW, 0.81 in SDC, and 0.89 in SDW (Supplemental Table S3). A stability plot based on the phenotype data (Figure 3b) revealed a grouping of the day-length-neutral lines in the lower left corner. The lines that did not head in SDW grouped in the top right corner. A group of early stable lines grouped in the lower left square above the red marked lines were all were selected in Iceland (line 55, 247_11; line 58, Skegla; line 57, Kria; line 54, 247_1; line 56, Hrutur) or the Faroe Islands (line 20, Tampar).

3.3 | Height

Temperature had a large effect on the average height (Figure 2; Supplemental Figure S4). Most of the lines had the tallest plants in LDC followed by SDC, LDW, and finally SDW. The broad-sense heritability for height was 0.95 in LDC, 0.96 in LDW, 0.89 in SDC, and 0.91 in SDW, (Supplemental Table S3). The difference in height between cold and warm and long and short day, respectively (Figure 2c) illustrated how most lines responded to temperature by expressing taller phenotypes in cold temperature vs. warm temperature irrespective of day length ($p \leq .001$). A few lines, however, had a different pattern, with the three extremely early Icelandic lines, 247_11, 247_1, and Hrutur, consistently producing the tallest plants in the short-day treatments (Figure 2c). The height effect was also visible on the spikes in these three lines, producing a larger inflorescence in short-day treatments (data not shown). The line JO_1279 (also known as cultivar Nord) had the most extreme temperature response in long-day environments, where it almost doubled its height in LDC compared with LDW (Supplemental Figure S4). A barley NIL, with a mutation at the semidwarf locus *Uzu*, was included in the panel, as it has previously been reported to be responsive to variations in temperature (Dockter & Hanssson, 2015). In the current study, the stability plot for height (Figure 3c) indicates that line 84, Bowman NIL Uzu1, had the largest CV, which confirms the strong response to temperature. Several lines in the lower end of the graph had very low CV (line 20, Tampar; line 26, IGP_M_268; and line 72, Teista II), indicating height stability throughout the environments.

3.4 | Population structure and GWAS

The PCA and the STRUCTURE analyses both showed a similar pattern of population structure (Figure 5; Supplemental Table S5) with the 57 six-rowed lines forming one cluster and the 27 two-rowed lines forming three clusters. The Bowman-derived NILs along with their mother cultivar Bow-

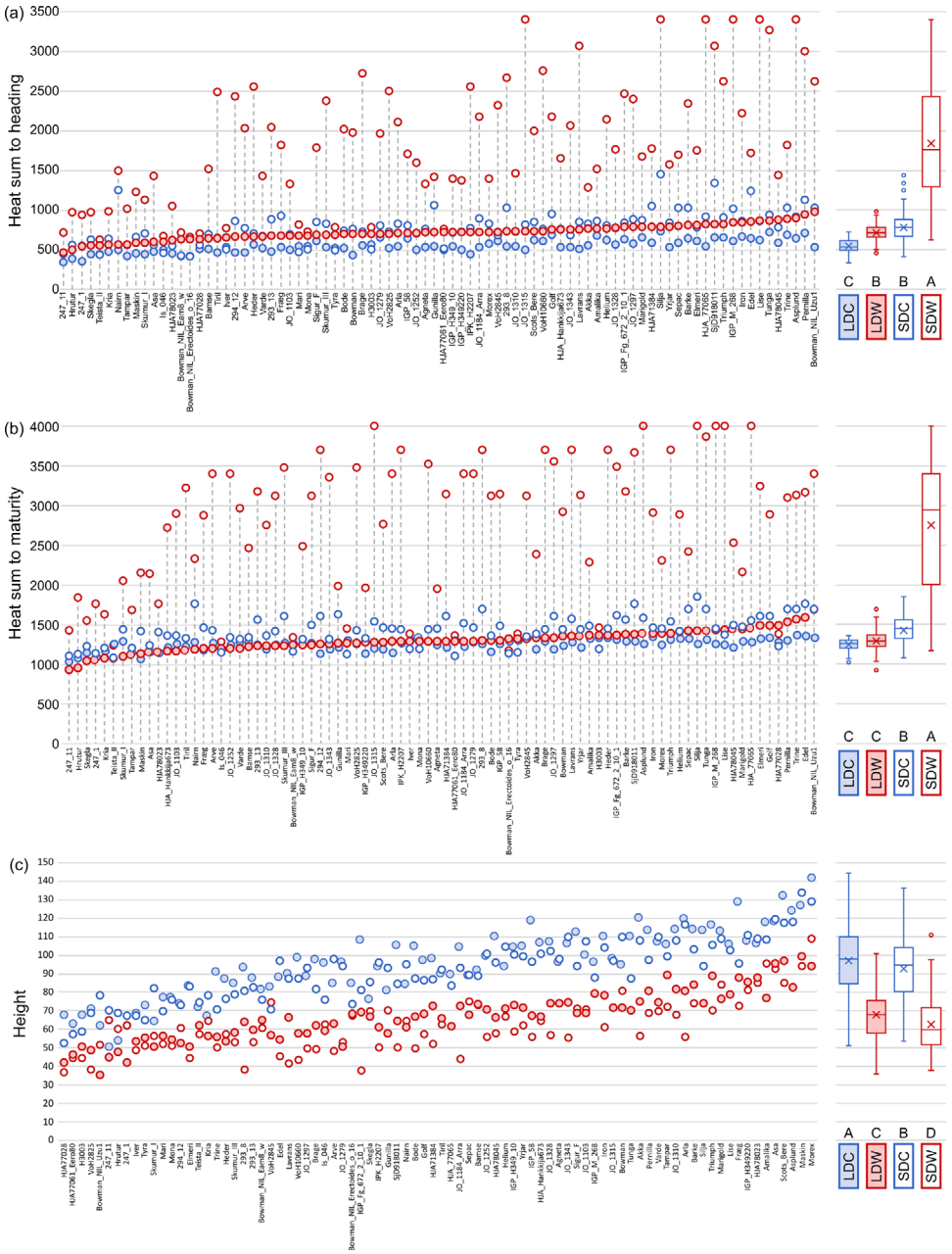

FIGURE 2 (a) Heat sum to heading (HSHD), (b) heat sum to maturity (HSMD), and (c) height for 84 spring barley lines grown in four environments: long day cold (LDC; 20-h day length and 15/5 ˚C, day/night; filled blue circles), long day warm (LDW; 20-h day light and 25/15 ˚C; filled red circles), short day cold (SDC; 12-h day length and 15/10 ˚C; open blue circles), and short day warm (12-h day length and 25/15 ˚C; open red circles). In (a) and (b), the genotypes tested are ordered from left to right based on the heat sum requirement under long day warm conditions, and in (c) they are ordered from left to right based on overall mean height from all environments. Fischer's least significant difference is indicated in the box plots, where means that do not share a letter are statistically significant

man formed one isolated cluster, and the remaining two-rowed lines formed two less distinct clusters. All day-length-neutral, two-rowed lines clustered together except for the two day-length-neutral NILs.

The GWAS analysis revealed 80 significant MTAs resulting in 21 QTL (Figure 6; Supplemental Table S6). For HSHD, eight significant MTAs were found; the most significant was in QDLT.1H.3, near (0.7 Mbp) the *Mat-a* locus, which was also the only one that showed effect in all four environments (Figure 7; Supplemental Table S6). This effect corresponded to 67 GDD, equal to 7 d in the cold treatments (or 3.5 d in the warm treatments). For HSMD, nine MTAs had a $-\log(p)$ value above the threshold (Figure 6b), half of which coincided with HSHD in one or more of the environments (Figure 7; Supplemental Table S6), but no significant association was consistent for all environments for the HSMD trait

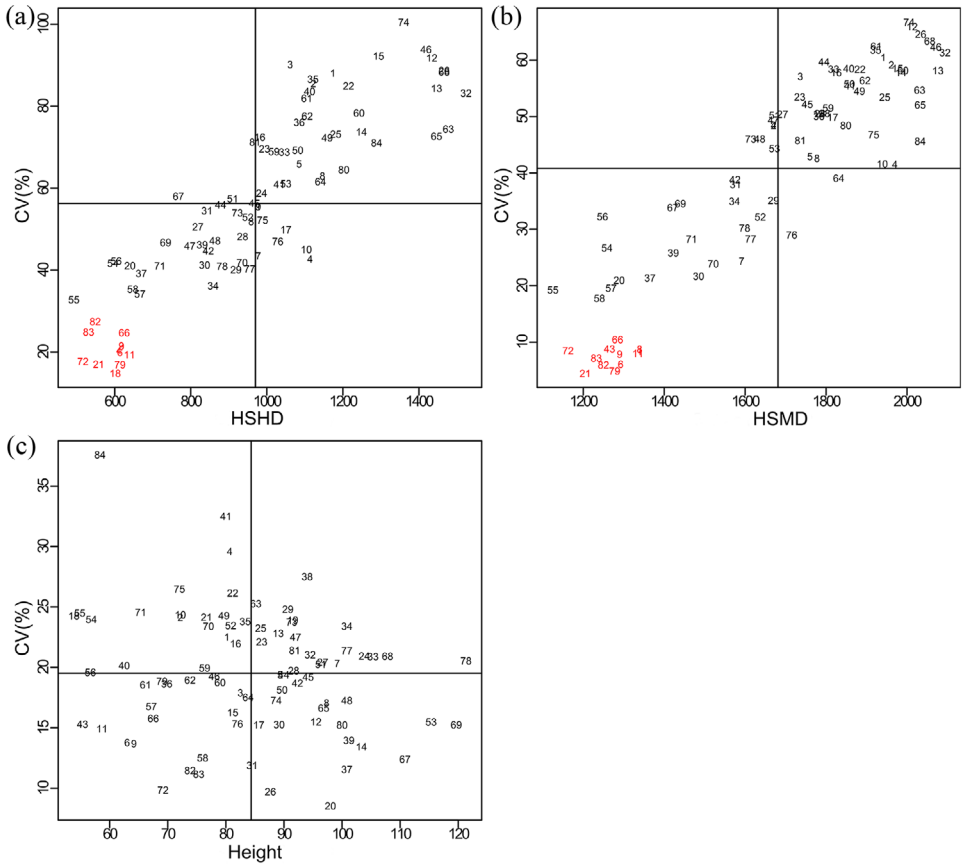

FIGURE 3 Stability plots showing the three phenotypic traits, (a) heat sum to heading (HSHD), (b) heat sum to maturity (HSMD), and (c) height plotted against the respective coefficient of variation calculated from the BLUE values from four environments: long day cold (LDC; 20-h day length and 15/5 ˚C, day/night), long day warm (LDW; 20-h day light and 25 /15 ˚C), short day cold (SDC; 12-h day length and 15/10 ˚C), and short day warm (12-h day length and 25/15 ˚C) (a) and (b), and the three environments LDC, LDW, and SDC in (c). The genotypes are plotted as numbers (1–84), the names of the corresponding genotype numbers can be found in Table 1. In (a) and (b), the 11day-length neutral lines are color coded in red

(Figure 7). In LDC, the most significant MTA was at QDLT.2H.1, physically located in the *Ppd-H1* gene, which had an effect of 140 GDD in LDC. In LDW the most significant MTAs for HSMD were found near the locus for *DHAR2* (0.3 Mbp), *Mat-a* (1.4 Mbp), and *FT1* (2.4 Mbp) (Figure 6b; Supplemental Table S6) with effects of 202, 175, and 50 GDD, respectively. For height, six significant associations were found, with SNPs located close to five known genes: *GA20ox1* (0.3 Mbp), *FTL5* (2.4 Mbp), *ARF19* (1.0 Mbp), *ARF4* (7.5 Mbp), and *EF-1a* (0.5 Mbp) (Figure 6c). The most significant association was found on chromosome 5H, located near (0.3 Mbp) the *GA20ox1* locus, which was also the only MTA for height that was consistent in all environments (Figure 7). The effect of the *GA20ox1* locus on height was 21 cm in LDC.

Only two MTAs for the three traits analyzed had an effect in all environments, for height, an MTA near *GA20ox1* (0.3 Mbp) and for HSHD near *Mat-a* (1.4 Mbp) (Figure 7), while a single MTA, found near the *denso/sdw1* locus (3.5 Mbp), had an effect in three different environments for HSHD. *Ppd-H1* (MTA located in the gene) was found in LDC for both HSHD and HSMD (Figure 7). An allele combination for the MTAs in the *Ppd-H1* (BK_16; 489 bp), and near the *Mat-a* (SCRI_RS_158298; 1.4 Mbp), and *FT1* (SCRI_RS_172761; 2.4 Mbp) loci explained 186 GDD for HSMD in the LDC environment, which corresponds to a maturity time 19 d earlier than the average (Supplemental Figure S5).

4 | DISCUSSION

The Icelandic environment poses challenges to crop production by the low temperature during the growth season. An extreme earliness in Icelandic barley lines has previously been reported (Göransson et al., 2019). The current study, for the first time, confirms the extreme earliness in a panel of barley lines developed for northern latitudes in controlled environments. It provides an important insight into the genetic mechanisms behind this early maturity and height stability that will enable a further expansion of cereal production northward. In this study, phenotypic data show that the heat sum

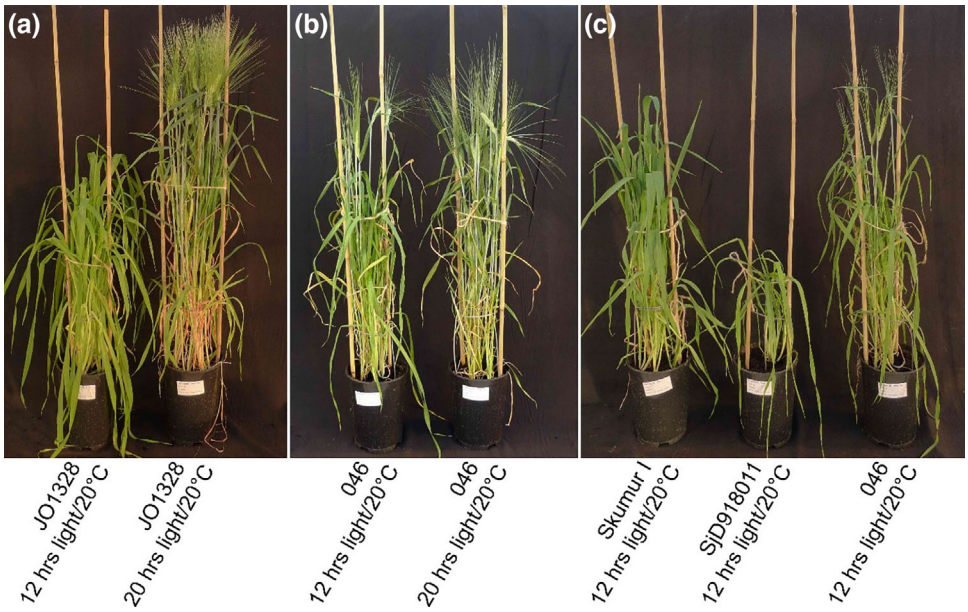

FIGURE 4 Examples of phenotypic differences in photoperiod response for plants grown in two environments: long day warm (LDW; 20-h day light and 25/15 ˚C) and short day warm (SDW; 12-h day length and 25/15 ˚C). (a) JO1328 growing in SDW (left) and LDW (right); (b) IS-046 growing in SDW (left) and LDW (right); (C) the mid-plant SjD918011 had severely delayed heading and stunted growth in SDW, whereas the left plant 'Skumur I' had delayed heading but normal growth, and the right plant, 046, was day-length neutral. All plants photographed 48 d after sowing

requirement to heading is consistently lower in LDC than in LDW for all lines ($p \leq .001$) (Figure 2a). Eleven genotypes were day-length neutral, of these two were NILs of cultivar Bowman with allelic variation in the *Mat-a* locus and nine Nordic genotypes, all of which descended from the induced mutant cultivar Mari, released in 1960 as an X-ray irradiated mutant of the Swedish cultivar Bonus (Gustafsson et al., 1971). Mari has been shown to carry a mutated allele in the *Mat-a* locus (Faure et al., 2012; Zakhrabekova et al., 2012). The locus with the strongest association to HSHD was *Mat-a* (Figure 6a; Supplemental Table S6), a locus known to infer day-length neutrality and previously proposed to infer adaptability to barley in diverse environmental conditions ranging from high altitudes in tropical regions to high latitude regions (Zakhrabekova et al., 2012). The locus was not found to be associated with heading in a previous study with similar material in field conditions (Göransson et al., 2019). In this study, however, with more contrasting environmental conditions, it was shown that nine of the Nordic barley genotypes included in the study indeed were day-length neutral, and all of them carried the same allele in the MTA for *Mat-a*. However, out of the 84 lines included, a total of 42 carried the same SNP allele, so it can be concluded that the MTA with the highest $-\log(p)$ value (SCRI_RS_158298) is not diagnostic for the day-length neutrality. A wider network of alleles is clearly at play, which is to be expected for a complex trait like heading. There was no clear pattern in heat sum requirements between cold and warm treatment under short-day conditions. The lines combining earliness with stability to environmental conditions (Figure 3a) had either a day-length-neutral allele in the *Mat-a* locus or were selected in Iceland.

Maturity in low temperature is the most important breeding goal in a cool maritime subarctic climate such as Iceland. There is often a long period during the grain filling period where temperatures slowly decline from the peak of 11 ˚C in July and August down to an average temperature of just above frost mark before harvest (Icelandic Meteorological Office). The panel showed three significantly different subgroups for relative HSMD in the long-day environments ($p \leq .001$): One group that followed the pattern for HSHD that is with a lower heat sum requirement in LDC than in LDW, one group with a similar heat sum requirement, and one group with a higher heat sum requirement in LDC than in LDW (Supplemental Figure S4B). Incidentally, the lines in the last group were largely the same as those showing the highest stability in height between LDC and LDW (Supplemental Figure S4). These lines, which are mostly Icelandic, have been selected in an environment similar to the LDC environment. The mean heat sum requirement of the first six lines in Supplemental Figure S4B were 1,159 GDD. This corresponds well with previously reported heat sum requirements to HSMD for early Icelandic barley of 1,200 GDD (Ólafsson et al., 2007). Göransson et al. (2019) found HSMD in field conditions in Iceland to vary between 1,019 to 1,418 GDD with the mean of 1,294 GDD for a panel of 180 commercial barley breeding lines of Nordic origin, where the earliest lines were Icelandic. The time of maturity in Icelandic field conditions coincides for these early lines with the end

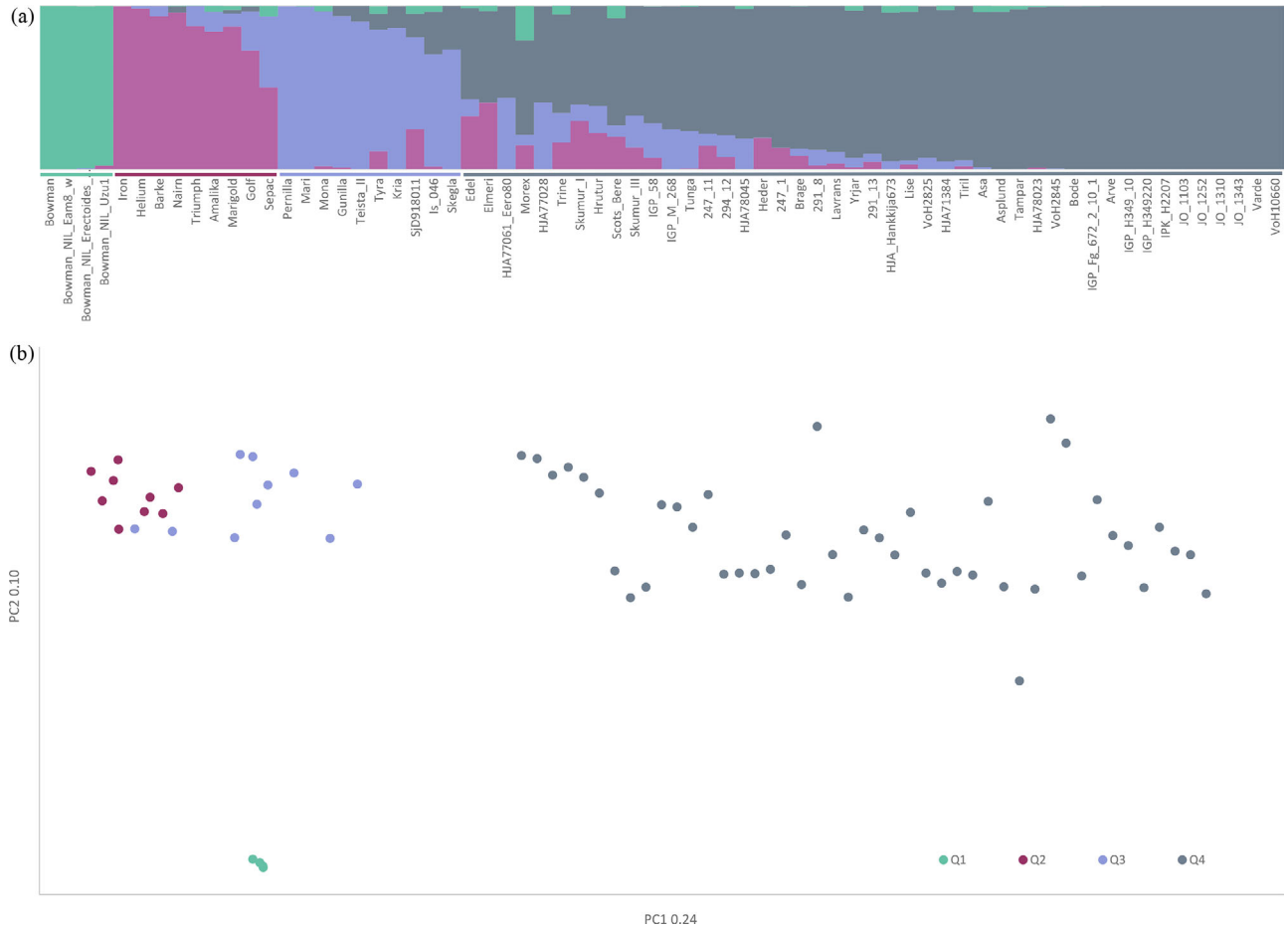

FIGURE 5 (a) Results of STRUCTURE analysis resulting in four subpopulations (color coded between the bar plot and the line names). (b) Principal component analysis (PCA) based on SNP markers grouped by STRUCTURE subpopulations (Q1–4). Q1, Q2, and Q3 where different constellations of two-rowed lines, and Q4 comprised of exclusively six-rowed lines

of the warmest summer period, in August. The reason why many Icelandic barley lines show a contrasting HSMD in cold vs. warm temperature (as seen in Supplemental Figure 4B) could be that they have been selected to head early, whereas less focus has been on their maturity time. The early heading could have led to the maturity occurring in the warmest season, leaving the early lines unexposed to the cold autumn temperatures to which later heading material had been exposed. In LDC, the strongest association with HSMD was with the *Ppd-H1* locus. The gene *Ppd-H1* is a major determinant of barley photoperiod response (Turner et al., 2005), with a dominant allele *Ppd-H1* most common in winter barley and a recessive *ppd-H1* allele more common in spring barley (e.g. 'Triumph' and most North European spring barley). The *ppd-H1* allele provides an adaptive advantage for the plant, which uses the spring to develop vegetatively instead of transitioning early to flowering in response to the increase in day length. The *ppd-H1* allele has previously been shown to be effectively fixed in Nordic spring barley (Göransson et al., 2019). However, the current panel had a higher frequency of the same lines that, in an earlier study, were shown to carry the sensitive allele but had been too few to enable detection through GWAS (Göransson et al., 2019). The allelic diversity in *Ppd-H1* seems to be interacting with other loci for the extreme earliness found in three Icelandic genotypes. An allele combination between *Ppd-H1*, *Mat-a*, and *FT1* with an average accumulated heat sum of 1,065 GDD for HSMD in the LDC environment (corresponding to 107 d) differed significantly ($p \leq .001$) from the overall mean of 1,251 GDD (corresponding to 125 d in LDC). We speculate whether the adaptation for low heat sum requirement to maturity involves GA regulation, and hypothesize that the earliest lines lack temperature sensitivity. Boden et al. (2014) found that the loss-of-function mutant of *Mat-a* has an increased expression of *FT1*, which was activated by the *GA20ox2* regulation of GA. Composite crosses maximizing the allelic diversity for the main earliness genes (especially the ones controlling the GA signaling pathway) could potentially create populations where this can be studied in more detail. It is interesting that *CEN*, a well-known earliness locus, did not show up in the GWAS. However, other studies have reported that a single allele of the *CEN* locus is virtually fixed in European spring barley (Tondelli et al. 2013;

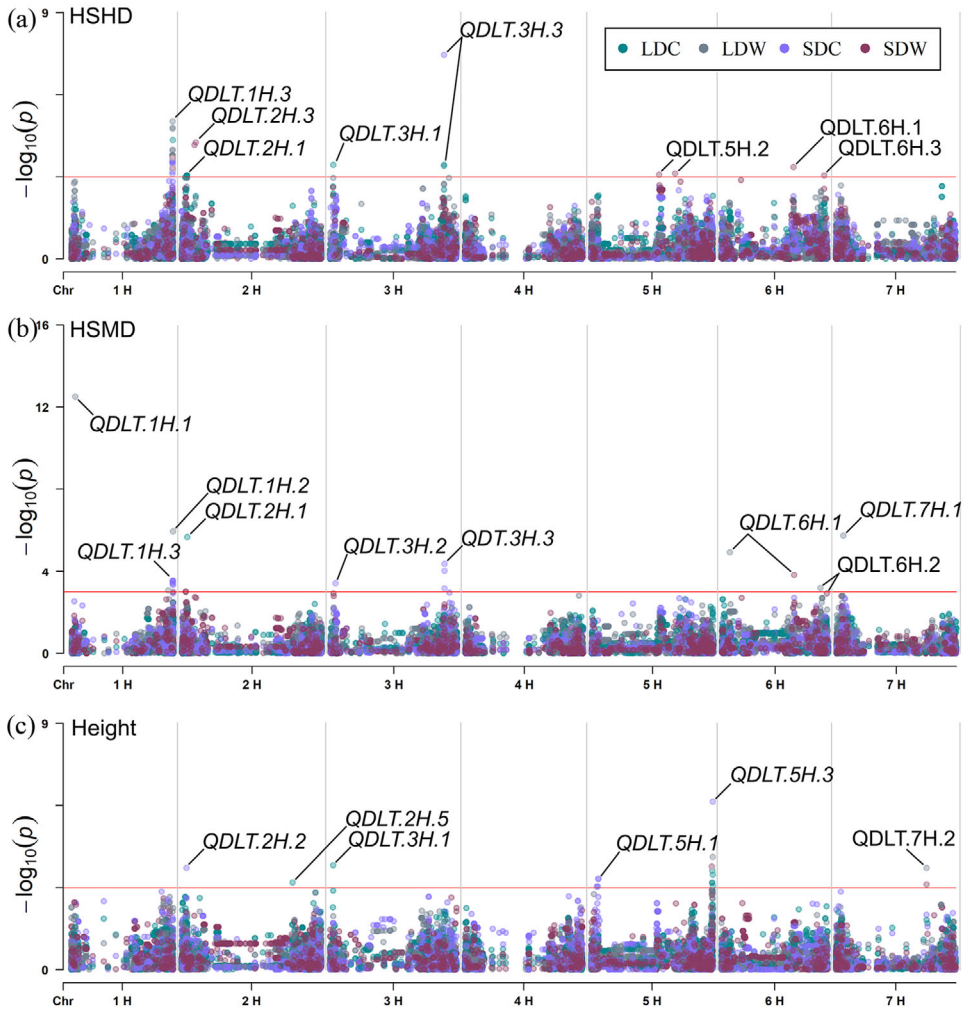

FIGURE 6 Manhattan plots showing significant associations for the traits (a) heat sum to heading (HSHD), (b) heat sum to maturity (HSMD), and (c) height in four environments: long day cold (LDC; 20-h day length and 15/5 ˚C, day/night), long day warm (LDW; 20-h day light and 25/15 ˚C), short day cold (SDC; 12-h day length and 15/10 ˚C), and short day warm (12-h day length and 25/15 ˚C). Quantitative trait loci are indicated and alternative putative loci can be found in Supplemental Table S6

Fjellheim et al., 2014; Göransson et al., 2019), which could explain why it was not found in the GWAS of the currently reported panel.

The study found that height varied mostly as a result of temperature and not day length. In low temperature, the plants grew taller (Figure 2c). However, a subset of lines of primarily Icelandic and Faroese origin showed a relative stability in height between the LDC and LDW environments. The phytohormone GA influences height and this has been used in barley breeding programs since the Green Revolution by incorporating semidwarf genes, which downregulates GA production (Xu et al., 2017), thus leading to shorter plants that can tolerate higher input of fertilizer without lodging. In Europe and North America, allelic variation at the *denso/sdw1* locus is most widely used to produce semidwarfing varieties (Jia et al., 2009). Allelic variation at the *denso* locus originating in the Danish cultivar Abed Denso and the Czech mutant cultivar Diamant, is allelic to the *sdw1* allele originating from the Norwegian cultivar Jotun (Jia et al., 2009). The *denso/sdw1* locus acts as a suppressor of GA and has been shown to be an ortholog of the rice *sd1* locus coding for the *GA20ox2* gene (Jia et al., 2009). Sakata et al. (2014) found that rice carrying the *GA20ox2* allele responsible for the *sd1* mutant showed hypersensitivity to low temperature for pollen development (which is regulated by the same semidwarf gene, *sd1*, that regulates plant height), which resulted in a disruption of the GA downregulation. The *GA20ox2* gene has a homologue, the *GA20ox1* gene, which has been reported to compensate for reduced function of *GA20ox2* (Xu et al., 2017). An MTA at the *GA20ox1* (*denso/sdw1*) locus was found to be significant in all environments, explaining an effect of 21 cm in LDC. All plants of the subset of lines showing height stability had the same *GA20ox1* allele, whereas both alleles were apparent for genotypes with high temperature response. We

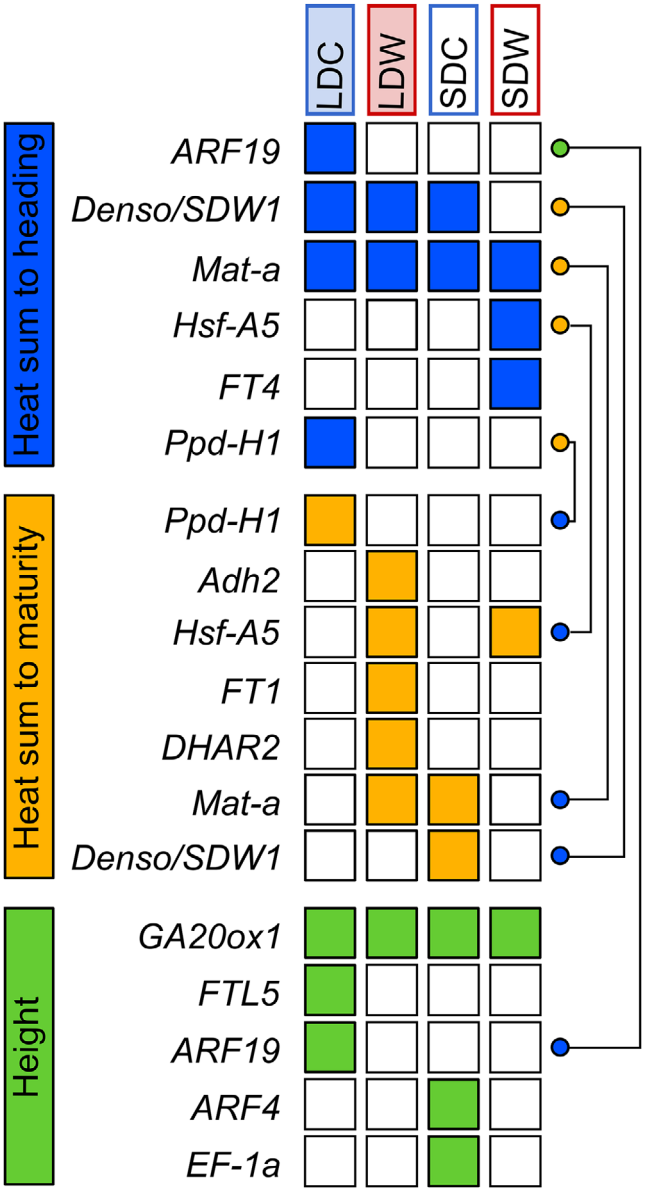

FIGURE 7 Overview of marker trait associations (MTAs) with putative loci and which of the four environments long day cold (LDC; 20-h day length and 15/5 ˚C, day/night), long day warm (LDW; 20-h day light and 25/15 ˚C), short day cold (SDC; 12-h day length and 15/10 ˚C), and short day warm (SDW; 12-h day length and 25/15 ˚C) they were found

speculate whether *GA20ox1* can compensate for the loss of function of *GA20ox2* in low temperature by downregulating GA production. However, as this was only seen in a subset of the genotypes with the same SNP for *GA20ox1*, more loci are presumably involved in this compensation. Interestingly, the genotypes with weakest height response, and hence highest height stability, to temperature were all selected in a cold environment. In particular, the temperature insensitive lines Teista II and Tampar qualify for further studies to reveal the genetics behind their height stability.

Two recent studies have performed GWAS on comparable panels of Nordic spring barley. Wonneberger et al. (2017) analyzed MTAs for heading and height in a set of Nordic spring barley lines grown under field conditions in Norway, and Göransson et al. (2019) performed GWAS for HSHD, HSMD, and height for another spring barley panel of Nordic origin grown under field conditions in the Nordic countries and Germany. The present study shared no identical MTAs with Wonneberger et al. (2017), whereas three MTAs were identical for both HSHD and HSMD, and one MTA for HSMD with the previous study by Göransson et al. (2019). The MTAs for both HSHD and HSMD were SCRI_RS_15171 (3H, *denso/sdw1*), SCRI_RS_164290 (3H, *denso/sdw1*), SCRI_RS_187343 (6H, *Hsf-A5*), and only for HSMD: SCRI_RS_193132 (3H, *denso/sdw1)*. The three markers on chromosome 3H were all localized near (<3.7 Mbp) the *denso/sdw1* locus. *Denso/sdw1* has previously been reported to influence height and heading (e.g. Jia et al., 2009). *Hsf-A5* is a drought and heat-stress regulator (Reddy et al., 2014) and interestingly, this MTA was only found in the warm environments where the highest temperatures were registered.

The accurate identification of MTAs for row type near the expected loci *Int-c* (0.3 Mbp) and *Vrs1* (0.9 Mbp) (Supplemental Table S6) provided confidence in the mapping results for other traits, even though the spring barley panel evaluated here is smaller than most comparable GWAS studies. The MTAs highlighted in the results were located within or near (<3.7 Mbp) previously known loci for the respective trait indicating that the peaks are true associations and not false positives. The PCA based on the genetic data showed a grouping according to row type. The day-length-neutral lines and the group with delayed heading in SDW did not form subgroups, indicating that this is rather an effect of few loci rather than an effect of the general genetic diversity. Heritability of the traits were similar or slightly higher than other recent studies (Göransson et al., 2019; Wonneberger et al., 2017), which found the broad-sense heritability for heading and height in field conditions to be in the range of 0.6–0.9. In controlled conditions like the current study, it is expected that the heritability is higher because of higher phenotyping precision. A controlled environment can never fully mimic field conditions. Nevertheless, a targeted selection in a northern environment has had impact on key traits. Icelandic barley lines showed a unique pattern of early maturity not found elsewhere and this can be partly assigned to an allelic difference in the *Ppd-H1* locus. Better understanding of the genetic mechanisms behind heading and maturity in low temperature in barley can work as a model for other crops when the production area is expanded northward. Such knowledge is essential for any breeding program where these are the main objectives, such as in Iceland. Looking past the present challenge when the tools for early maturity and height stability are available, the focus could be moved to combine these traits with more

quality traits and/or try to improve the yield of these cultivars. Many Icelandic lines lacked temperature induced stem elongation in low temperature, which was otherwise widely observed in the Nordic barleys studied. This is an advantage in the windy and cool Icelandic environment where the barley plants would otherwise be prone to lodging during the grain-filling period before harvest. This stresses the importance of selecting breeding lines in the target environment. The combination of *GA20ox1* and *denso/sdw1* (*GA20ox2*) has an impact of height control in low temperature, and furthermore the interaction of *Ga20ox1* with known earliness loci merits further studies. A validation of these results in field conditions with a larger panel would be necessary to fully conclude this pattern. Another way would be to construct a segregating population with diversity in the three *GA20ox* loci to further explore their effects on height and earliness in cold temperature.

ACKNOWLEDGMENTS

The study was financially supported by the Norwegian Genetic Resource Centre (Norsk Genresurssenter), the Research Council of Norway (NFR grant 224833) and Graminor. Thanks to gardeners and technicians at NMBU for maintaining the plants in the greenhouse and to Anne Guri Marøy for assisting with DNA extractions. Thanks to Roland von Bothmer (SLU) for supplying the original seed from the Nurminiemi et al. (1996) collection. Thanks to NordGen for providing seeds for the study. Thanks to the anonymous referees for constructive comments.

AUTHOR CONTRIBUTIONS

Magnus Göransson: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Validation; Visualization; Writing-original draft; Writing-review & editing. Jón Hallsteinn Hallsson: Formal analysis; Methodology; Supervision; Visualization; Writing-original draft; Writing-review & editing. Therése Bengtsson: Data curation; Formal analysis; Methodology; Software; Validation; Visualization; Writing-original draft. Åsmund Bjørnstad: Conceptualization; Methodology; Supervision; Writing-review & editing. Morten Lillemo: Conceptualization; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Validation; Writing-original draft; Writing-review & editing.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

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

How to cite this article: Göransson M, Hallsson JH, Bengtsson T, Bjørnstad Å, Lillemo M. Specific adaptation for early maturity and height stability in Icelandic spring barley. *Crop Science*. 2021;*61*:2306–2322. https://doi.org/10.1002/csc2.20459