Going against the grain

Evaluation of a pre-breeding material for adaptation of oats to Icelandic conditions

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Abstract

Common oat (*Avena sativa* L.) is a cereal crop grown in temperate climates worldwide. In the Nordic countries, oat production comprises a significant part of food and forage production, yet the domestic oat production in Iceland today is limited. The production is under threat as the most popular oat cultivar in Iceland is about to be withdrawn from the market. In the absence of cultivars adapted to the extreme Icelandic environment, growth in the sector is limited. In this work, the Iowa Recurrent Selection Population (IRS) was evaluated as a potential pre-breeding material for oats adapted to Icelandic conditions. A seed panel of 445 genotypes sourced from novel recurrent selection material, experimental lines and commercially available cultivars were used to collect phenotypic data under field conditions in Iceland. Recorded data on days to panicle emergence and degree of maturity at harvest was used for analysis of earliness, as incomplete maturation within the short Icelandic growing season hinders successful production. Plant height and lodging susceptibility was recorded to assess the ability of the material to withstand strong winds and rain.

Observations from a field trial conducted by the Norwegian University of Life Sciences (NMBU) conducted on the same seed panel were compared with the Icelandic data to assess dynamic stability, phenotypic diversity and genotype by environment interaction (GxE). Additionally, a genome-wide association study (GWAS) was carried out to identify genetic markers associated with the traits of interest. The broad-sense heritability was high for two of the four studied traits. Moreover, the genotypic variation for all traits was large, indicating great potential for high genetic gain though further breeding. Putative marker-trait associations were found for six individual SNPs and three traits. The results from a principal component analysis (PCA) indicated considerably larger genetic diversity within the IRS population compared to the cultivars and experimental lines. This suggests that the IRS population could present valuable genetic resources for broadening the currently narrow Nordic oat gene pool.

Trends of increased height, delayed panicle emergence and decreased degree of maturity was observed over cycles of selection in the IRS population. Although the experimental lines and cultivars surpassed the IRS population in overall performance, certain genotypes within the IRS population exceeded the mean values and showed great promise as candidates for future pre-breeding of Icelandic oats.

Keywords: oat, *Avena sativa*, panicle emergence, broad sense heritability, Nordic oats, Iceland, pre-breeding, GxE

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Abbreviations

ATS	Accumulated temperature sum
BLUE	Best linear unbiased estimator
BLUP	Best linear unbiased predictor
GWAS	Genome-wide association analysis
GxE	Genotype-by-environment interaction
H^2	Broad-sense heritability
IRS	Iowa Recurrent Selection population
LbhÍ	Landbúnaðarháskóli Íslands
Lsmeans	Least-square means
MAF	Minor allele frequency
NMBU	Norwegian University of Life Sciences
PCA	Principal component analysis
PE	Panicle emergence
QTL	Quantitative trait locus
QQ-plot	Quantile-Quantile plot
Std Dev	Standard deviation
SNP	Single nucleotide polymorphism
SLU	Swedish University of Agricultural Sciences
SS	Sum of squares

1. Introduction

Common oat, *Avena sativa* L., is a multipurpose cereal crop, cultivated for the grain which is used for human consumption and livestock feed as well as silage and forage (Butt et al. 2008). Globally, it is the seventh most cultivated cereal crop in terms of economic importance worth approximately six and a half billion dollars (FAO 2022b). Together with other cereal species, oats belong to the *Poaceae* family (Baum 1977). Oats are self-pollinating crops, and the inflorescence is distributed in the form of a loose panicle that differs in morphology from the upright growing spikes of other cereals such as rye, barley and wheat (Ladizinsky 2012).

1.1 Genetics

Oats are allohexaploid (2N=6x=42) with the chromosomes distributed across three subgenomes, denoted as AACCDD (Peng et al. 2022). The subgenomes are proposed to have emerged through hybridization and polyploidization, resulting in a genome with a large number of repetitive segments and translocations. Due to the subgenomes being difficult to distinguish from each other as a result of the complex genome structure, gene annotation and chromosome assignment have proven challenging. Subsequently, mapping and whole genome sequencing of oats has been time-consuming, causing oat research to fall behind that of other cereal crops (Finnan et al. 2019). The first fully annotated reference genome of oats was published by Kamal et al. (2022), consisting of an assembly of the Swedish oat cultivar Sang. A complete whole genome sequence assembly of the *A. sativa* ssp. *nuda* landrace variety Sanfesan was published shortly after by Peng et al. (2022). In 2024, the International Oat Nomenclature Committee proposed a universal nomenclature system for the genome (Jellen et al. 2024). Prior to this, varying annotations were used across different studies, hindering comparisons (Jellen et al. 2024).

In light of these advances, opportunities for utilisation of genomics-driven breeding approaches such as marker assisted selection and genomic selection have become possible in breeding programs (Wight et al. 2024). The use of genomics in breeding is relatively new and will prove an important tool in the rapid development that is required to adapt crop cultivation to changing conditions that climate change might

entail (Singh et al. 2021). In recent years, several studies have identified quantitative trait loci (QTL) related to important agronomic traits in oats (Wight et al. 2024).

1.2 Cultivation history and geographic extent

Oats are considered to be the youngest cereal, with evidence suggesting domestication around 1000-0 B.C (Zhou et al. 1999). Wheat, believed to be the oldest cereal, is estimated to have been domesticated more than 10 000 years ago (Ahmed et al. 2023).

The demand for oats as fodder declined during the 20th century, mainly due to the mechanization of agriculture and invention of the automobile, leading to decreased production and acreage (He & Bjørnstad 2012; Fogelfors 2015). This decrease was further amplified by oats being abandoned for higher yielding crops such as wheat and barley (Grau Nersting et al. 2006). As an effect, the number of oat breeding programs declined, making oats a less attractive crop due to fewer new high performing cultivars on the market (Leišová-Svobodová et al. 2019).

In recent years, the demand for plant-based options to dairy products has led to a regained interest in oats (May et al. 2020). Further, oats have emerged as a cereal with several health benefits, creating a surging demand among producers and consumers (Sola 2019; Levitt 2023). Compared to other cereals, oats are rich in protein, healthy fats and dietary fibre, and recent studies have demonstrated that a consumption of oats can reduce cholesterol levels, blood pressure, and glycaemic index (Murphy et al. 2004; Butt et al. 2008; Tang et al. 2023). The rise in interest of oats as a healthy food has led to new breeding aims such as grains with improved B-glucan, protein or oil content (Gazal et al. 2014). Oats have also surfaced as a good source for ingredients suitable in cosmetics and skincare products due to anti-inflammatory and barrier repairing properties (Wollenberg et al. 2018; Fazer group 2023). This recent demand for oats create new opportunities to increase Nordic oat cultivation and export (Ceplitis 2019).

The production of oats mainly takes place between latitudes of 40° and 60°N in North America, Europe and Asia (Buerstmayr et al. 2007). The total cultivation area in the world was in 2022 estimated at 9.5 million hectares of arable land (FAO, 2022a). Oats are successfully grown in temperate climates with excess precipitation and poor edaphic conditions due to their ability to adapt to different marginalized environments (Leišová-Svobodová et al. 2019; Hakala et al. 2020). Through the release of new photoperiod insensitive cultivars, cultivation in areas that do not fulfil the photoperiod requirements of photosensitive variants is now possible.

The most widely cultivated species within the *Avena* genus is *A. sativa L.*, even though cultivation of black oats (*Avena strigosa*) and red oats (*Avena byzantina*) in form of landraces or locally adapted cultivars do occur (Fogelfors 2015). Hull-less oat varieties are sparsely grown, mainly in China (Li et al. 2015). This phenotype is defined by the lack of shell around the kernel, which is of interest to producers since no dehulling is required. The phenotype is believed to have emerged from a mutation causing a variation in the *N1* gene (Yan et al. 2020).

1.3 Oat production in the Nordic countries

Due to being a long day crop, oats are well suited for cultivation in high latitude conditions, and thereby production in the Nordic countries (here defined as Denmark, Finland, Iceland, Norway and Sweden). Oats have been grown in Scandinavia since the Bronze Age but became economically important in the late 19th century (Fogelfors 2015). Production peaked at this time, at about one million hectares cultivated in Sweden alone, constituting 70% of the country's total food export (Murphy & Hoffman 1992). The Nordic oat production followed the earlier mentioned trend of decreased cultivation as a result of declined fodder demand (Fogelfors 2015). As a result, Nordic oats have not followed the same trend of increase yield potential as barley (Öfversten et al. 2004; Hakala et al. 2020). In Scandinavia, oats are mainly grown as a spring sown crop, whereas sowing in the autumn occurs in areas with milder winters on more southern latitudes (Kim et al. 2014). In Scandinavia, oats are sown in spring when soil conditions become favourable, in April or May. The growth stage in which the panicle becomes visible above the leaves, the panicle emergence (PE), typically occurs in late June (Fogelfors 2015).

The Nordic countries have in recent years become frontrunners in the production of plant-based dairy alternatives (Brink 2023). Swedish Oatly, Finnish Fazer and Oddlygood are among the major producers of oat products in the world. Despite the large domestic production, import of oats to the Nordic countries is still substantial (FAO, 2022c). Together with the rising demand, this presents a significant opportunity for an intensified domestic production of oats.

Breeding of oats started early in Scandinavia, and locally adapted landraces were largely abandoned in favour of cultivars bred for improved yield and increased diseace resistance (Grau Nersting et al. 2006; Leino 2017). However, this sucessful breeding resulted in less population heterogeneity, and parts of the genetic variation related to adaptaion to diverse environment were lost (Leino 2017).

1.4 Oats in Iceland

Iceland's history of modern arable farming is recent and domestic grain production only started in the 1960s (Sigurbjörnsson 2014). At this time, barley cultivation was made possible due to the introduction of a domestic breeding program, focusing on creating cultivars with early heading. An interest in producing oats in Iceland has surfaced in recent years. Landbúnaðarháskóli Íslands (LbhÍ) has been conducting continuous research on oats since 2017, focusing on the identification of cultivars with early PE, early maturity, and high yield quality. Efforts have been made to establish oat production in Iceland, and as of today, there is one commercial oat producer (mbl.is 2018).

Two main hurdles are preventing an increased oat production in Iceland: the lack of avalible cultivars adapted to the climate as well as processing facilities. The cultivation is entirely depended on the import of seed, since no domestic oat breeding or seed production takes place in Iceland. The preferred oat cultivar today is Swedish cultivar Cilla, developed and maintained by Lantmännen. This cultivar is considered moderatly early, but lacks qualities needed to ensure a stable large scale production under extreme conditions. However, Cilla has been difficult to import and other alternative cultivars are needed. For Icelandic oat production to become successful, the infrastructure must be in place for processing the grain. In order to establish an infrastructure, there must be reliable cultivars available for farmers.

1.5 Important traits for adaptation to Icelandic conditions

1.5.1 Earliness

Oats are grown all over temperate parts of the world, but temperate zones still contain abiotic variations that need to be considered when developing oats for specific regions (Trevaskis et al. 2022). In subartic areas, low temperatures during spring and early summer results in delayed sowing and slow germination, posing a major barrier for crops to achieve full maturity (Carlson-Nilsson et al. 2021). The cool summers in Iceland limit the day degrees needed for oats to reach maturation within the growing season. Varieties that are considered early maturing in other Nordic countries may still not mature fast enough under Icelandic conditions (Hilmarsson & Svavarsdóttir 2019). Harvesting oats before full maturation reduces yield and quality, making the grain unsuitable for human consumption.

Earliness is a way to describe genotypes with a short growing period, and a tendency to reach PE and maturation relatively early. Differences in genetically determined sensitivity to environmental factors such as photoperiod and temperature causes variation in this trait (Buerstmayr et al. 2007). In general, early cereal cultivars are utilised in cooler areas with short growing seasons, such as the UK and northern Europe, but are also common in areas where earliness is desirable to avoid drought or pest problems during grain filling (Plotnikov et al. 2024).

The term earliness describes a rapid development rate, taking both genetic and environmental factors into account. "Earliness per se" is a narrower definition, describing the variation in trait expression that remains when environmental factors have been excluded, i.e. when light and heat demands have been fulfilled (Mroz et al. 2023). However, studies have shown that earliness per se is not completely independent of environmental factors. Cereal crops tend to develop faster under conditions with high temperatures, and low temperatures cause an extended period between PE and anthesis (Ochagavía et al. 2019). Developmental rate is therefore mainly dependent on the temperature, but variation in the response and sensitivity to the temperature still differ between genotypes.

Regulating the duration of the vegetative phase in cereals is a complex interaction between several genes (Trevaskis et al. 2022). Among these are genes regulating sensitivity to photoperiod (*Ppd*), vernalisation response (*Vrn*) and earliness per se genes (*Eps*). Among wheat germplasms adapted to different environments, the variations in the Eps genes are large, highlighting these factors' role in adaption (Ochagavía et al. 2019). Variations in the *Ppd* genes are causative for photo insensitivity in wheat and barley, a trait which through breeding has been tailored to enable cultivation in southern latitudes where the photoperiod requirements for photosensitive cereal are not fulfilled (Zhang et al. 2023). Although the *Ppd*, *Vrn*, and *Eps* genes have been extensively studied in other cereals crops such as wheat and barley, only putative homologs to *Vrn* have been identified in oats (Nava et al. 2012). As of today, most of the photo-response mechanisms involved in oat phenology remain unknown (Trevaskis 2022).

The interaction between factors affecting earliness is complex and tend to impact the expression of other agronomical traits such as vernalisation requirements and plant height (Plotnikov et al. 2024). It is therefore crucial to consider these factors not only when breeding for early cultivars, but also in regard to the earliness's influence on other agronomical traits.

1.5.2 Phenology

Phenology is a way to describe crop development rate through variation in timing between life cycle events (Trevaskis et al. 2022). By tailoring a crop's phenology through breeding, new varieties suited for various environments and different growing windows can be developed. A short development cycle would allow for oats to mature within the Icelandic growing period and in warmer climates, shorter cycles could allow for two crops per season (Zimmer et al. 2018). Further, rapid development is correlated to decreased plant height (Buerstmayr et al. 2007; Boczkowska et al. 2016; Haikka et al. 2020). Decreased height is desired in cereal since a shorter straw is proven to correlate with increased straw strength. Further, a decreased plant height limits the resources used by the plant for vegetative growth (Rabieyan et al. 2024). The yield potential in oats is closely connected to its growth cycle and development through the timing of PE and grain filling (Trevaskis et al. 2022). This is controlled by genotype-dependent responses to abiotic factors such as temperature and photoperiod. It is therefore important to consider yield when breeding for earlier oats, and to aim for a good balance between desired cycle length and yield.

1.5.3 Genotype-by-environment interaction

The term genotype-by-environment interaction (GxE) describes the fraction of a genotype's response to different environments due to genetic factors (Bernardo 2002). A genotype inhibiting high GxE will demonstrate a large variation in trait expression under different environmental conditions. When developing cultivars able to withstand varying or extreme conditions, it is important to take GxE into consideration in effort to minimize negative effects on performance caused by the environment. Maintaining low GxE is necessary when adapting crops to fluctuating weather conditions, as is the case in Iceland.

The broad-sense heritability (H^2) is utilized to estimate the proportion of phenotypic variance due to genetic factors among genotypes in a population (Bernardo 2002). Hence, if a heritability score were to be 1, all variation is dependent on the genotype, no variation is caused by the environment and no GxE has occurred. A common misconception is that heritability is a way to compute how much of a trait is determined by genes (Oldenbroek & van der Waaij 2014). Heritability is instead an indicator of genetic variation, an evaluation of how well the trial design is able to account for spatial variations and to estimate the expected response to selection.

There exists a trade-off between high grain yield and yield stability in oats (Helms 1993). Previous selection has largely focused on high yields under optimal environmental conditions, and not necessarily yield security under suboptimal

conditions. A large ability to adapt to different environments has been defined by Becker and Léon (1988) as “dynamic stability”. A high dynamic stability is associated with a low degree of GxE.

A relatively new factor influencing breeding aims is climate change (Kole 2020). Possible consequences of climate change are decreased temperatures and heavy rains, and to ensure stable yields under such suboptimal conditions, new cultivars adapted to harsh climates are needed (Carlson-Nilsson et al. 2021). With a changing climate, dynamic stability is a crucial component that needs to be considered in breeding programmes, since oat yield is greatly influenced by external conditions. The extreme environmental condition in Iceland creates substantial demands on a crop’s ability to adapt. A high dynamic stability is there for crucial for successful breeding and cultivation in this region.

1.5.4 Lodging and plant height

The Icelandic climate is characterised by strong winds and heavy precipitation, which increasing the risk of lodging. Lodging occurs when the straw of a crop bends or folds, causing the crop to lean. Usually, lodging occur in autumn under the pressure of wind and rain. This results in decreased yield quality, yield loss or even total crop failure. Lodging is highly correlated with plant height and stem width, hence, a crop with a short and robust straw is less inclined to lodge (Tumino et al. 2017; Nakhforoosh et al. 2020). Even though plant height is proposed to be the most important factor on lodging resistance in cereal, other characteristics such as stem width, stem strength and root system strength also contributes (Liu et al. 2024; Rabieyan et al. 2024). Height is a complex trait (Würschum et al. 2014), heavily influenced by abiotic factors such as nutrient and water availability (Manghwar et al. 2024). In order to develop crops resilient to lodging, more research is needed on the interaction between plant height, straw composition and environmental conditions.

1.6 Breeding for a novel environment

1.6.1 Pre-breeding and base broadening

Throughout history, crops have been selected for desired traits to enable cultivation in specific areas (FAO 2015). Before the agrarian revolution, this selection was carried out locally by choosing to propagate plant material proven suitable for the specific location (Carlson-Nilsson et al. 2021). This type of informal selection resulted in a broad spectrum of landrace populations that evolved over time in response to specific climates and environmental conditions (Leino 2017).

A populations's resilience and ability to adapt to a varying environments is heavily influenced by its genetic diversity (Newton et al. 2010). As an effect of selection, the genetic diversity in breeding populations has become narrowed (FAO 2015). A prerequisite for successfull breeding programs is genetic variation in target traits. In order to develop resilient crops suitable for extreme conditions, novel genetic material must be introgressed into breeding populations. To achieve this, it is necessary identify promising prebreeding material for base-broadening of the gene pool and determine germplasm sources for traits of interest within the existing gene pool.

The diversity in Nordic oats is relatively low compared to oats grown in other areas of the world (Grau Nersting et al. 2006; Achleitner et al. 2008; Tinker et al. 2009). This poses a problem considering the increased breeding demands. The common cultivars grown in Scandinavia today originate from a few breeding lines developed from landraces (He & Bjørnstad 2012). Therefore, introgression of material from other gene pools is crucial for further improvement of Nordic oats, since the loss of diversity has caused variations in traits such as earliness to decrease.

Possible sources of material for base-broadening are the wild relatives of crops and landraces carrying traits that have been lost during breeding processes with specific focuses (Mohler et al. 2023). While modern cultivars have been selected for homogeneity, landraces are characterized by heterogeneity and, along with wild relatives, could therefore serve as valuable sources for reintroducing trait variation.

1.6.2 The Iowa recurrent selection population

In the 1990s, the Iowa recurrent selection population (IRS) was developed through a collaboration between the Iowa State University and the Agricultural University of Norway, as described by Holland et al. (2000). The IRS population was developed with the aim to create a genetically diverse population adapted to diverse environments without inflicting any yield penalties. To achieve this, 20 germplasms of North American and Scandinavian origin were selected as parental lines based on their performance in yield trials conducted in Iowa and Norway. Of these 20 lines, 11 were commercially available cultivars originating from both continents, including two daylight-insensitive cultivars, one of which also carried the hulless trait. The remaining parental lines consisted of experimental lines developed by Iowa State University. Out of these nine experimental lines, seven contained introgressions from wild oat, *Avena sterilis*.

The main focus of the study was to determine whether the dynamic stability, adapatation to diverse environments and yield thorugh recurrent selection could increase simoultaniously (Holland et al. 2000). Holland et al. were able to

demonstrate a yield increas both within and across environments over the course of three selection cycles. Selection was carried out by choosing genotypes with high grain yield within and across environments. Compared to the original population mean, the total yield increased by 2.6 % per cycle. Yield stability increased in later cycles of selection, suggesting that recurring selection can increase the dynamic stability. Holland et al. (2000), reported results from three cycles of selection. As of today, the same material has gone through another three cycles of selection. In 2022, the IRS population was evaluated and phenotyped in field by NMBU. Until then, the material had not been utilised since early 2000s, apart from occasional field multiplications.

1.7 Aims

The aim of this study was to evaluate the Iowa Recurrent Selection Population's potential as pre-breeding material for oats adapted to Icelandic conditions. Additionally, the study aimed to identify genetic resources for the earliness trait.

Field trials conducted in Iceland and Norway provided data on traits of interest, including PE, maturity, plant height, and lodging. To determine whether the evaluated material is suitable for further breeding efforts of oats resilient to Iceland's extreme conditions, the following research questions were adressed:

- Is the variation in trait expression and genetic diversity in the material sufficient for further pre-breeding efforts?
- Does trait expression and genetic diversity differ between selection cycles?
- Is the dynamic stability of the material sufficient for uniform performance under extreme environmental conditions or will excessive genotype-by-environment interaction be demonstrated (GxE)?
- Are the broad-sense heritabilities of the studied traits high enough to ensure satisfactory genetic gain through further selection?
- Can marker-trait associations be identified for traits of interest in order to facilitate future breeding of early-maturing oats?

The main goal was to support the cultivation of oats in Iceland. The results of this research provides new information on the performance of oats under Icelandic conditions and will facilitate future oat breeding.

2. Material and methods

2.1 Phenotypic analysis

2.1.1 Plant material

A seed panel of 445 genotypes (presented in Appendix 1) was used in Iceland. The main part consisted of genotypes belonging to the IRS population (397 genotypes). The IRS population was developed through recurrent selection by Holland et al. (2000). Over cycles, the yield increased both within and across environments. This material was chosen for evaluation in Iceland due to its proposed high dynamic stability. The IRS population genotypes in the seed panel evaluated in consisted of parental lines (P) and genotypes representing four cycles of selection, denoted as C0, C2, C4 and C6. To evaluate the IRS population's relative performance, 11 commercially available cultivars of Nordic and North American origin were added to the panel, together with 37 experimental lines developed by NMBU for improved fat, protein or B-glucan content. These three groups comprising the seed panel will henceforth be referred to as the *IRS population*, *cultivars*, and *experimental lines*. Included among the cultivars in the panel was Swedish cultivar Cilla, which was chosen as check for the Icelandic trial.

2.1.2 Field trials

Field trials were carried out in Hvanneyri, Iceland (64°33'N 21°46'W), at the Hvanneyri Agronomic Research Centre (HARC), and at NMBU's research centre in Ås, Norway (59°40'N; 10°46'E). A map of trial site locations was created in ArcGIS Pro (Esri 2024) and is shown in Figure 1. All 445 genotypes included in the Icelandic seed panel were evaluated in Norway, except for the cultivar Cilla.

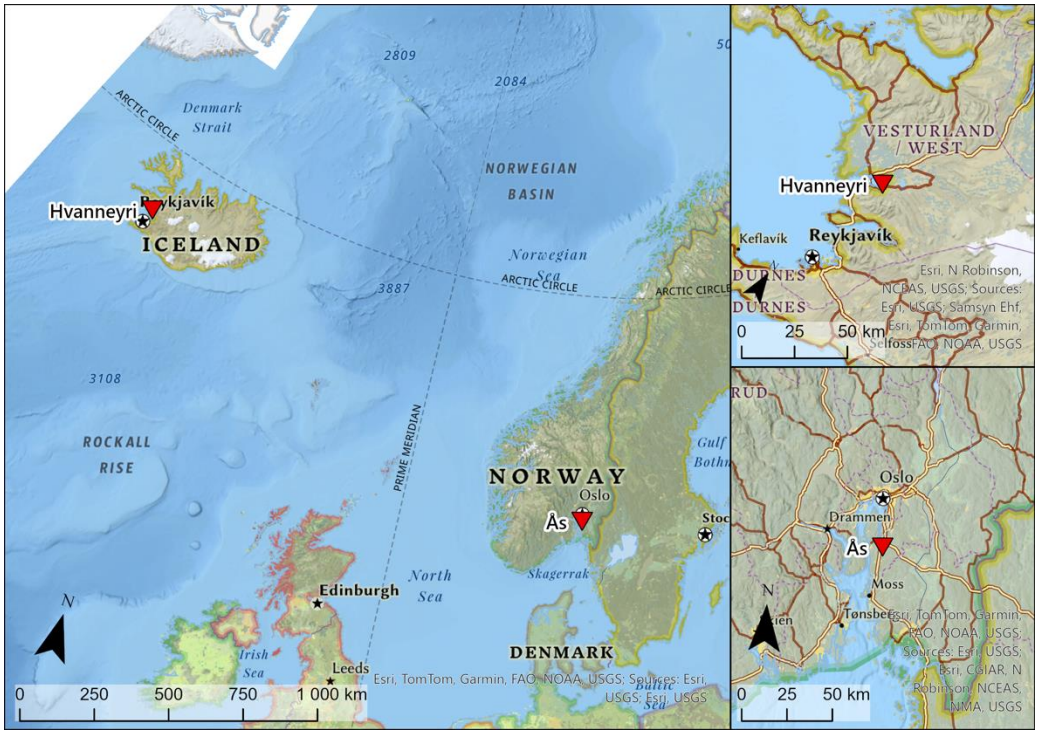

Figure 1. Map indicating the locations of the two trial sites (marked with red arrows) in Hvanneyri, Iceland and Ås, Norway.

An Alpha Lattice design created in R package Agricolae (Mendiburu & Yaseen 2020) implemented in the R statistical software (R Core Team 2022) were used in the trial conducted in Iceland. The layout consisted of two replications with a total of 900 plots. The plots were distributed over 60 blocks and 15 columns, each plot measuring 0.5 m^2. Circa 10-12 g of seed were used per plot.

In Iceland, sowing took place on the 29th of April 2023 in a field that had been ploughed and harrowed. The trial was fertilised with 67 kg nitrogen ha^{-1}. In plots that were empty due to error in the trial preparation, Cilla was used as replacement. The trial was harvested in two rounds; replication one was harvested on the 4th of October, and replication two on the 11th of October. The corresponding trial in Norway was conducted using an alpha lattice design. Sowing occurred on the 15th of May, and harvest on the 17th of September.

2.1.3 Field evaluations in Iceland

To evaluate earliness, the number of days from sowing to PE together with maturity scores at time of harvest were recorded in Iceland. PE was considered as achieved when 50% of all plants within a plot had 50% of their panicles visible. Degree of maturity was determined at harvest, based on a scoring index ranging from one to nine, defined in Table 1.

Table 1. Scoring index used in the trial in Iceland for assessment of maturity.

Score	Definition
1	Plot completely green
2	< 20% of the plants in the plot is yellowing
3	>30% of the plot or the plants in the plots have commenced yellowing
4	The whole plot is yellow halfway up or up to panicles
5	>95% of the plot has yellowed. Still no signs of full maturation
6	<30% of the plot completely mature
7	>50% of the plot is completely mature
8	>80% of the plot is completely mature
9	100% of the plot has matured

Lodging susceptibility was assessed in Iceland on the 3rd of October, using a scoring index provided by LBHÍ, defined in Table 2. The index accounts for frequency and severity of lodging within each plot. Lodging scores collected in Norway were expressed as percentage of the plot affected by lodging.

Table 2. Scoring index used in Iceland for lodging severity assessment.

Score	Definition
1	No lodging or leaning, all straws upright
2	<15% of straws are leaning
3	<30% of plants in the plot are lodging, but the angle of leaning is not high
4	<40% of plants in the plot are lodging, with a high angle of leaning
5	>50% of plants in the plot are lodging with the straw touching the ground, or 100% of the plot is leaning
6	>95% of plants in the plot are lodging
7	100% of plants in the plot are lodging, no straws touching the ground
8	>95% of plants in the plot are lodging, and half of the straws are touching the ground
9	>95% of plants in the plot are lodging and touching the ground

Plant height was measured in Iceland on the 23rd of August by placing a measuring stick at the base of each plot and visually assessing the mean canopy height of the entire plot. By this date, all plots had completed the stem elongation phase.

2.1.4 Phenotypic data provided by NMBU

From the corresponding field trial conducted in Norway, raw phenotypic data together with means calculated by accounting for spatial variations in the field were provided by NMBU. Traits phenotyped in Norway were days from sowing to PE, plant height, lodging and days from sowing to maturity. In Norway, days from

sowing to maturity were recorded to assess maturity. Normalized scoring indexes were created to enable analysis of traits for which the scoring methods differed between trial locations. The first plot to mature were assigned a score of 100 and the last plot were assigned a score of one. Similarly, the most mature genotype in Iceland were assigned a score of 100, and the least mature genotype a score of one. For lodging, the scoring index used in Iceland took both lodging severity and area of plot lodging into consideration. The scoring index used in Norway accounted only for the percentage of lodging plant within each plot. Observations recorded in Iceland were therefore scaled to range between 0 and 100, with a score of zero corresponding to an Icelandic index score of one (no occurrence of lodging in plot) and 100 corresponding to an original score of 9 (all plants severely affected by lodging). Normalized scoring indexes are presented in Appendix 2.

2.2 Climate conditions

Meteorological data for daily precipitation and mean temperatures captured by the weather station at HARC in Iceland were provided by the Icelandic Met Office (Veðurstofa Íslands). Corresponding values from the weather station in proximity to the Norwegian trial site were downloaded from Norsk Landbruksmeteorologisk Tjeneste (2023). The accumulated temperature sum (ATS) per day during the growing season in each location was calculated with a base temperature set at 5°C. These sums were matched to each genotype's mean PE date to display ATS by the time of panicle emergence. Similarly, the ATS related to the number of days to maturity for the Norwegian genotypes were calculated and matched. Photoperiods during the growing season for each location were obtained using the NOAA Solar calculator (Global Monitoring Laboratory 2023). Photoperiod per day during the growing season was calculated as hours from sunrise to sunset.

2.3 Genotyping

435 accessions represented in the seed panel were genotyped by Lantmännen in partnership with NMBU. Genotyping on samples from harvested seed material in the Norwegian trial was carried out using a single nucleotide polymorphism (SNP) array method, using customized 7K-SNP chip (Polley et al. 2023).

2.4 Data analysis

2.4.1 Statistical Analysis

The phenotypic data was analysed using linear and mixed models. Models were fitted in R statistical software (R Core Team 2022), using the package lmer4 (Bates et al. 2015). Models providing the best fit were chosen based on residual plot information, analysis of variance (ANOVA), the Akaike Information Criterion (AIC) developed by Akaike (1974) and the Bayesian Information Criterion (BIC) developed by Schwarz (1978). The AIC and BIC are criteria used to assess the most suitable number of parameters to use in a model, in order to reduce the risk of over- or underfitting while maintaining simplicity. To create figures and illustrations, the R package ggplot2 was used (Wickham 2016). To compare phenotypic values for maturity and lodging across environments, normalised scales were used in models including both trial locations.

For descriptive statistics and comparison between the trials, the least squares means (lsmeans) were calculated separately for each location. Lsmeans for the Icelandic trial was derived from model (*a*):

$$Y_{iklmn} = g_i + R{:}B_{kl} + R{:}C_{km} + T_n + e_{iklmn}$$

The best linear unbiased estimators (BLUEs), used as phenotypes in the GWAS, were calculated across locations using model (*b*):

$$Y_{ijlmn} = g_i + L_j + L{:}R_{jk} + L{:}B_{jl} + L{:}R{:}C_{jkm} + e_{ijlmn}$$

where Y is the phenotype for genotype g_i planted within location L_j, replicate R_k, row B_l and column C_m, and e is the corresponding error. T_n is the effect of small blocks containing two by 20 plots. Capitalised letters indicate random effects, while lower case letters represent fixed effects.

ANOVAs were conducted to determine the relative contributions of genotype, environment and estimated GxE variance to the phenotypic variation. For this analysis, the following models were used (*c*, *d*):

$$Y_{ijk} = (gl)_{ij} + L{:}R_{jk} + e_{ijk}$$

$$Y_{ijk} = l{:}r_{jk} + D_{ij} \cdot l_j + e_{ijk}$$

where D_{ij} denotes the random effect associated with the slope of L_j for each G_i.

To estimate the genotypic and phenotypic variance the best linear unbiased predictors (BLUP) were extracted from the model (*e*):

$$Y_{ijklm} = l{:}r_{jk} + G_i + L{:}B_{jl} + L{:}C_{jm} + e_{ijklm}$$

Broad-sense heritability (H^2) within and across trials was calculated to enable comparison of genetic stability across environments. This was estimated through:

$$H^2 = \frac{\sigma_G}{\sigma_P}\text{Variance}$$

where σG is the genotypic variance and σP is the total phenotypic variance. For comparison of mean values for each trait per group and cycle, a model including the selection cycle (C_o) was used (*f*):

$$Y_{jkmo} = (cl)_{jo} + L{:}R_{jk} + e_{jkmo}$$

Pearson correlation analysis of traits across locations was conducted on extracted BLUEs using the ggpairs function from R package ggplot2 (Wickham 2016). For comparison of trait expression within and between locations, the lsmeans for each separate location were used.

2.4.2 Association analysis

Prior to distribution, an initial quality control of the genotypic SNP data had been carried out by NMBU. Monomorphic markers had been culled, and samples filtered for a call rate of ≥90%.

An unpublished consensus map used for marker positioning was provided by NMBU alongside the genotypic data. Data regarding genotypes not present in either the Icelandic seed panel or the provided genotypic data was deleted. Markers that had lost polymorphism after sample filtering were removed from the final data set. Further, markers not present in the consensus map were removed, as well as duplicate markers.

Association mapping was carried out through a genome-wide association study (GWAS) through the GAPIT3 package by Wang and Zhang (2021) with the R statistical software (R Core Team 2022). FarmCPU (Liu et al. 2016) was chosen as the model for the analysis based on comparison of quantile–quantile plots (QQ-plots) generated in GAPIT from iterated tests of several models. QQ-plots for FarmCPU are shown in Appendix 3. The estimated BLUEs across locations derived from model *b* were used as phenotypic values in the analysis. Based on scree plots from a principal component analysis (PCA) conducted in GAPIT, the first six principal components (PC) were included as covariates in the GWAS model to

account for potential population structure bias. In the final analysis, the minor allele frequency (MAF) threshold was set to ≤ 0.05 to avoid false positives. SNPs were considered significant when surpassing the Bonferroni threshold adjusted by GAPIT. A scatter plot of PC 1 and 2 was created from eigenvalues derived from the GWAS analysis and visualised in R package CMplots (Yin 2024). The linkage groups from the provided consensus map were matched against the common oat chromosome nomenclature proposed by Jellen et al. (2024). Overall MAFs per group and MAF of significant SNPs were calculated in Excel (Microsoft Corporation 2024) and visualised through previously mentioned graphic packages in R.

3. Results

3.1 Climate

On the 21st of June, at first PE in Norway, the ATS had reached 407°C, and 152°C in Iceland (Figure 2). The first PE in Iceland occurred on the 19th of July, with an ATS of 306°C in Iceland and 739°C in Norway. The first plot to mature in Norway did so on the 7th of August, with an ATS of 925°C in Norway and 429°C in Iceland. By the time of harvest in Iceland, the ATS was 658°C. Photoperiods peaked at 21.5 hours in Iceland and 18 hours in Norway.

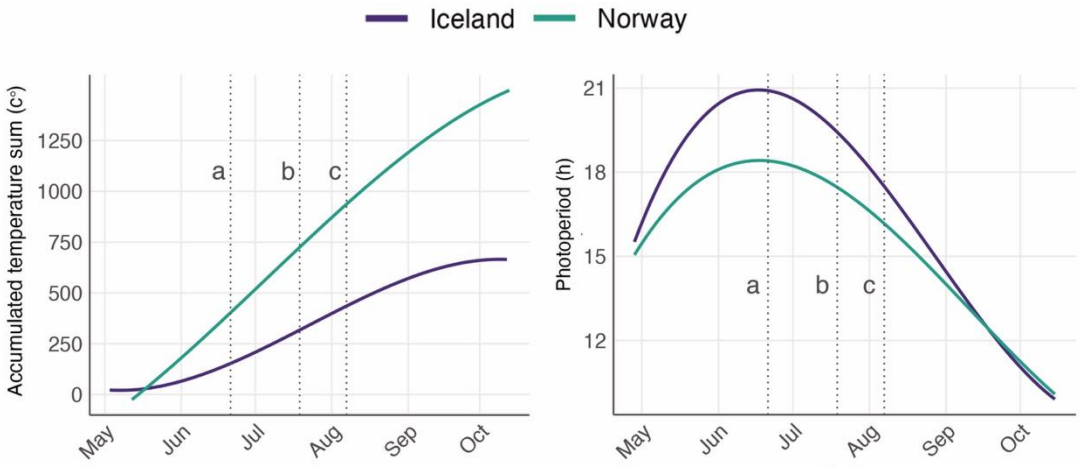

Figure 2. Accumulated temperature sum (C°) and photoperiod (h) in Iceland and Norway during the growing season. Vertical lines correspond to a) date of first panicle emergence (PE) in Norway, b) date of first panicle emergence (PE) in Iceland, c) date of first plot to reach maturation in Norway.

3.2 Phenotypic evaluation

3.2.1 Panicle emergence

PE in Iceland took place between the 19th of July (82 days after sowing) and the 15th of August (110 days after sowing), spanning a period of 27 days. The corresponding period in Norway was 14 days (Figure 3). The first PE in Iceland took place 41 days later than in Norway, expressed as the number of days from sowing in Iceland. The mean PE in Iceland occurred 94 days after sowing. Cilla's mean PE occurred 91 days after sowing. Mean PE in Norway occurred 47 days after sowing. In Iceland, genotype IA93247 (C2) exhibited the earliest PE (82 days after sowing) and IA96317 (C4) exhibited the latest (102 days after sowing). Both IA93247 and IA96317 belong to the IRS population. In Norway, the earliest genotype experimental line Y877-4-2 (41 days after sowing) and the latest the cultivar Matilda (53 days after sowing). Within the IRS population in Iceland, 42 genotypes exhibited earlier PE than Cilla.

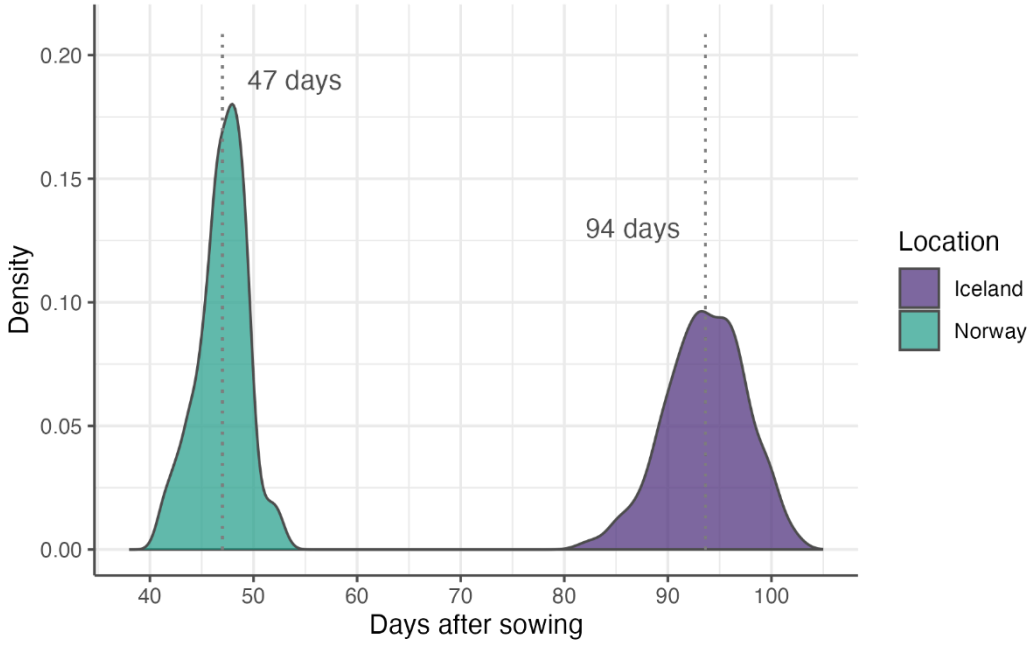

Figure 3. Density plot illustrating mean panicle emergence (PE) and total period of PE in Iceland and Norway, expressed in days from sowing to PE.

According to Model *c*, the genetic effect for PE contributed to 90% of the total sum of squares (SS) for all groups except for the experimental lines (95%; Table 3). The GxE variable explained between 0-0.5% of the variation and was significant for all groups.

Table 3. Fraction of variance in panicle emergence (PE) explained by covariates in Model c. G_i *denotes genotype i grown in location* L_j*, while* $G{:}L_{ij}$ *captures the interaction between genotype i and location j.* R_{jk} *represents the nested effect of replicate k within location j.*

	Full panel		IRS	
Variable	Sum sq %	P-value	Sum sq %	P-value
G_i	90	<0.001	90	<0.001
L_j	10	<0.001	10	<0.001
$G{:}L_{ij}$	0.03	<0.001	0.03	<0.001
$L{:}R_{jk}$	0.01	<0.001	0.01	<0.001
Residuals	0.02		0.01	

	Cultivars		Experimental lines	
Variable	Sum sq %	P-value	Sum sq %	P-value
G_i	95	<0.001	90	<0.001
L_j	5	<0.001	10	<0.001
$G{:}L_{ij}$	0.00	<0.05	0.05	<0.001
$L{:}R_{jk}$	0.01	<0.001	0.01	<0.001
Residuals	0.01		0.03	

The mean PE per group and cycle according to Model f is illustrated in Figure 4. In both locations, the earliest mean PE was observed for the experimental lines after 90 days from sowing in Iceland and after 45 days from sowing in Norway. The latest PE was observed for cycle 4 of the IRS population, with a mean of 95 days in Iceland and 48 days in Norway. The Pearson correlation coefficient of PE between locations, which assesses the similarity of responses among genotypes, was $r = 0.75$ (Figure 5), indicating a significant correlation ($p < 0.05$).

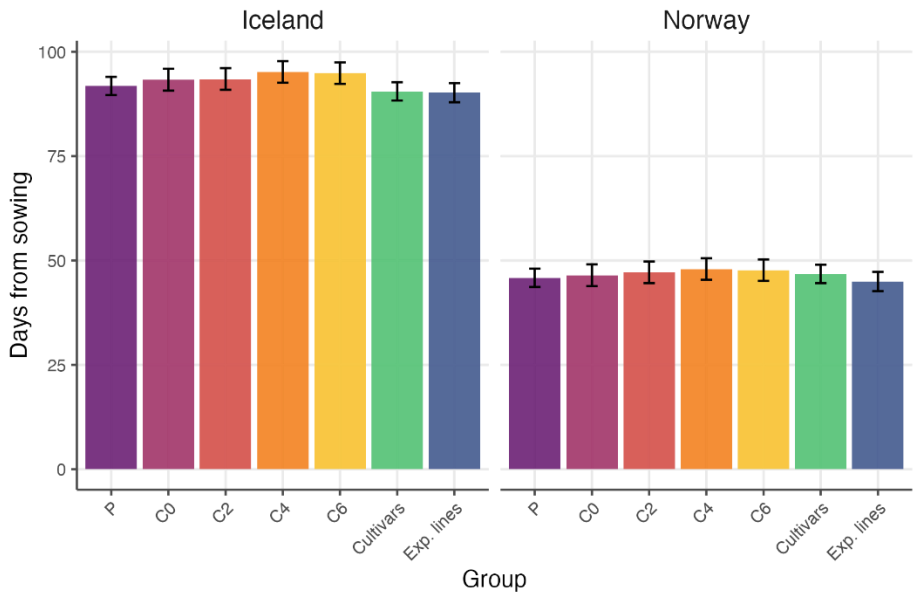

Figure 4. Differences in mean panicle emergence (PE) per group and selection cycle in Iceland and Norway, derived from Model f.

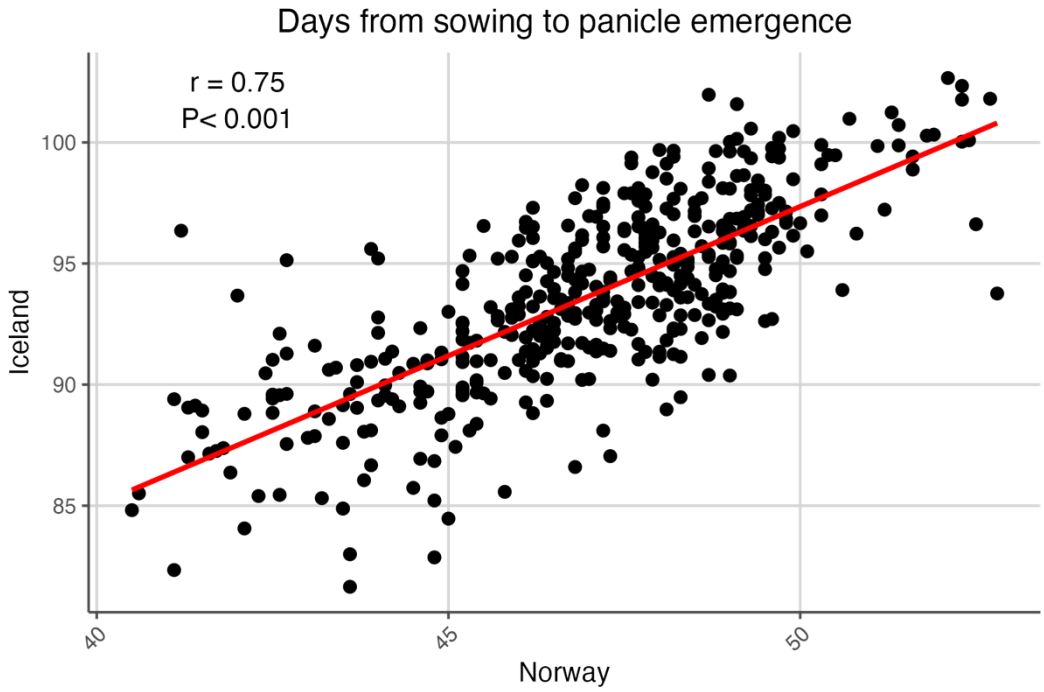

Figure 5. Scatter plot illustrating the significant Pearson correlation coefficient (r=0.75) for panicle emergence (PE), expressed in days from sowing to PE, between Iceland and Norway.

As indicated by Model *d*, the observed variance for PE was 14.06 in Iceland and 4.81 in Norway (Appendix 4). The genetic correlation was estimated at 0.84. H^2 for the full panel was 0.69 across locations, with values of 0.83 in Iceland and 0.89 in Norway. The cultivars exhibited an H^2 of 0.72 across locations, experimental lines 0.56 and the IRS population 0.69.

3.2.2 Maturity

Scoring of degree of maturity was conducted in Iceland at the time for harvest. Scoring took place on the 3rd of October, 160 days after sowing. At this time, six plots were fully mature (score 9, Table 1), of which four contained IRS genotypes, namely IA91146, IA91300, IA98538 and parental line Munin. The other two genotypes to have reached maturation were experimental lines D947-9-8 and Y930-4-6. Mean normalized maturity score for the entire Icelandic trial was 47 (Figure 6), and 69 for Cilla. In Norway, the first plot matured on the 7th of August, and the last on the 28th of August. Mean maturity score in Norway was 69. The first plot to mature in Norway did so on the 7th of August, corresponding to 88 days from sowing. The last plot reached maturity on the 28th of August, 109 days after sowing. Within the IRS population in Iceland, 22 genotypes exhibited higher maturity scores than Cilla.

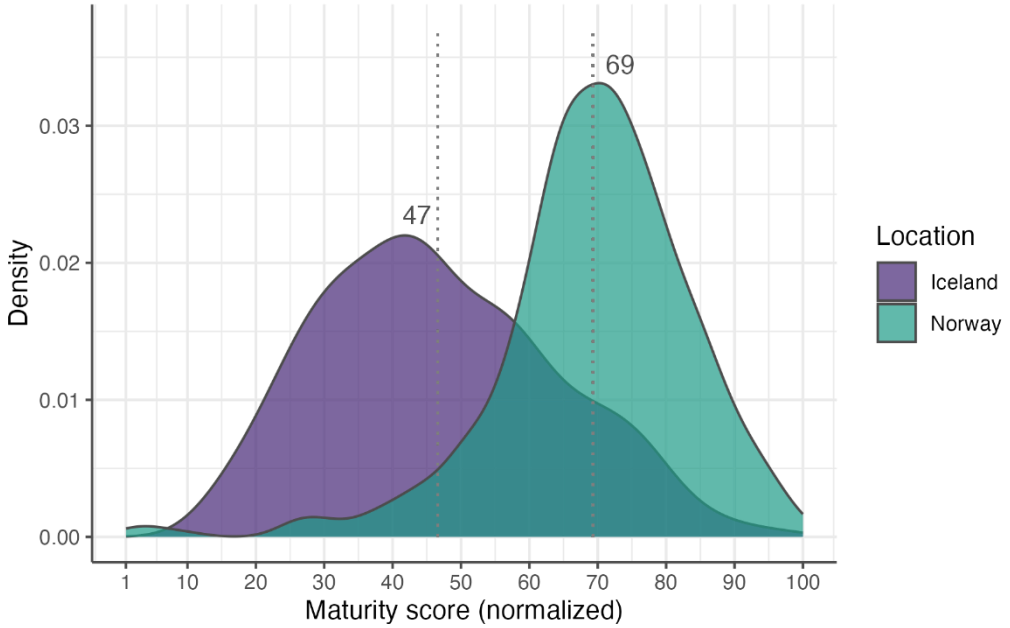

Figure 6. Density plot illustrating the distribution of normalized maturity scores and mean maturity scores in Iceland and Norway.

According to Model *c*, the genetic effect contributed to 91% of the total SS for maturity in the full panel and the IRS population (Table 4). The genetic effect was 94% for cultivars and 95% for experimental lines. The GxE variable explained between 0.5-1% of the variation and was significant for all groups.

Table 4. Fraction of variance in normalized maturity score explained by covariates in Model c. G_i *denotes genotype i grown in location* L_j*, while* $G{:}L_{ij}$ *captures the interaction between genotype i and location j.* R_{jk} *represents the nested effect of replicate k within location.*

	Full panel		IRS	
Variable	Sum sq %	P-value	Sum sq %	P-value
G_i	91	<0.001	91	<0.001
L_j	6	<0.001	6	<0.001
$G{:}L_{ij}$	1	<0.001	1	<0.001
$L{:}R_{jk}$	0.3	<0.001	0.3	<0.001
Residuals	1		2	

	Cultivars		Experimental lines	
Variable	Sum sq %	P-value	Sum sq %	P-value
G_i	94	<0.001	95	<0.001
L_j	4	<0.001	2	<0.001
$G{:}L_{ij}$	0.5	<0.05	1	<0.05
$L{:}R_{jk}$	0.4	<0.01	0.3	<0.001
Residuals	1		1	

The mean maturity scores per group and selection cycle according to Model *f* are illustrated in Figure 7. In both locations, the highest mean maturity scores were observed for the experimental lines, 62 in Iceland and 84 in Norway. The lowest mean maturity score in Iceland was that of cycle 4, with a score of 40. In Norway, the cultivars exhibited the lowest maturity with a normalized score of 74. The Pearson correlation coefficient of maturity between locations was r=0.45 and significant ($p<0.05$; Figure 8).

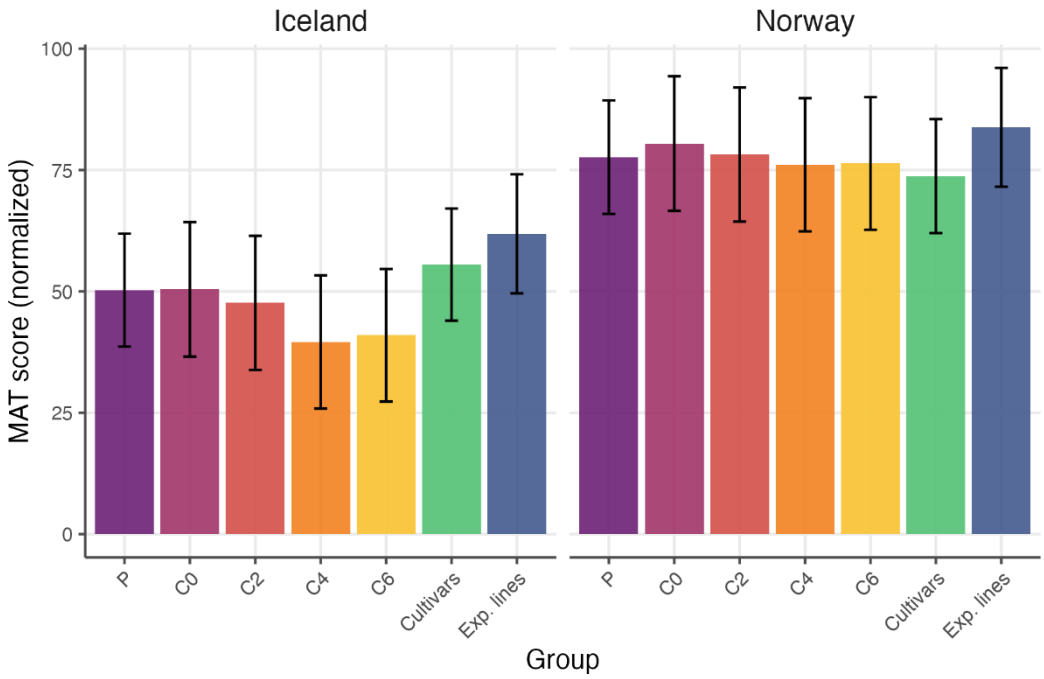

Figure 7. Differences in maturity scores per group and selection cycle in Iceland and Norway, derived from Model f.

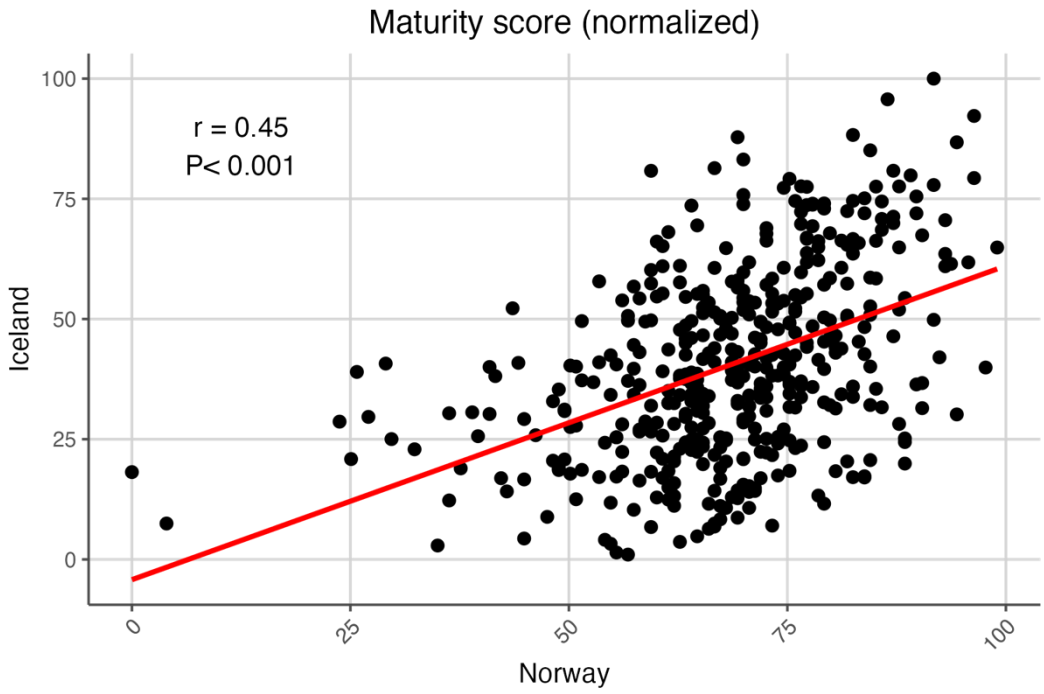

Figure 8. Scatter plot illustrating the significant Pearson correlation coefficient (r=0.45) for normalized maturity scores between Iceland and Norway.

As indicated by Model *d*, the observed variance for maturity was 249.3 in Iceland and 29.9 in Norway (Appendix 4). The genetic correlation was estimated at 1. H^2 for the full panel was 0.37 across locations, with values of 0.51 in Iceland and 0.47 in Norway, respectively. The cultivars exhibited an H^2 of 0.64 across locations, experimental lines 0.30 and the IRS population 0.34

3.2.3 Plant height

Plant height ranged between 61 and 118 cm in Iceland, spanning 57 cm (Figure 9). Mean plant height in Iceland was 93 cm, and 81 cm for Cilla. Mean plant height in Norway was 85, and observations ranged between 57 and 116, spanning 59 cm in total. The shortest genotype in both locations was A80004-2, belonging to the parental lines. The tallest in Iceland was genotype IA96407 of cycle 4 (122 cm), and in Norway experimental line X2-1 (117 cm). Within the IRS population in Iceland, 33 genotypes exhibited shorter plant heights than Cilla.

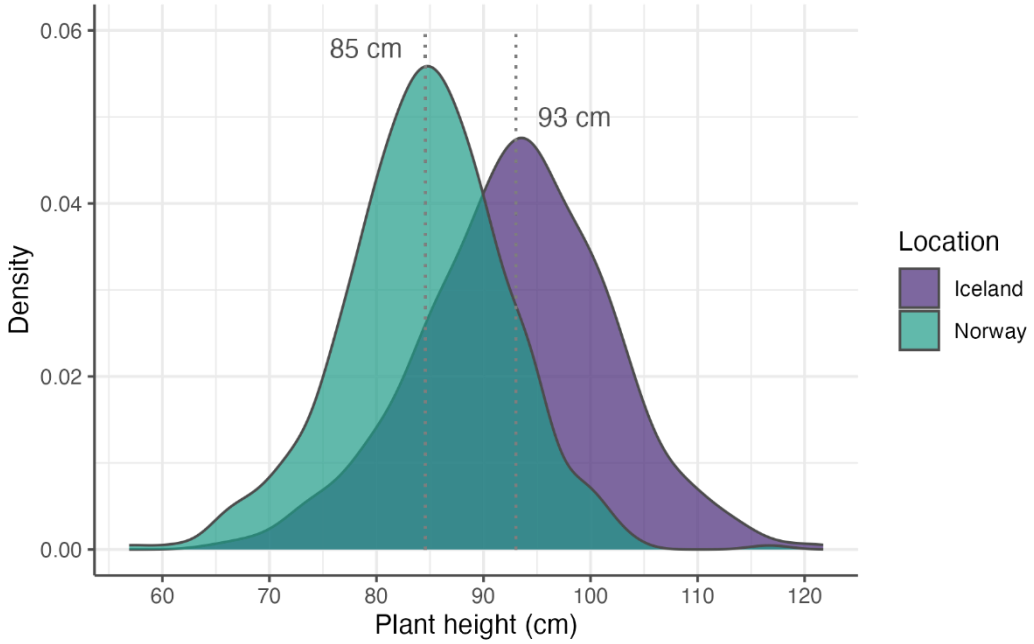

Figure 9. Density plot illustrating the distribution of plant height observations and mean plant heights, expressed in cm, in Iceland and Norway.

According to Model *c*, the genetic effect contributed to 99% of the total SS for plant height in all groups (Table 5). The GxE variable explained between 0.2-0.4% of the variation and was significant for all groups except for the experimental lines.

Table 5. Fraction of variance in plant height explained by covariates in Model c. *G_i denotes genotype i grown in location L_j, while $G{:}L_{ij}$ captures the interaction between genotype i and location j. R_{jk} represents the nested effect of replicate k within location j.*

	Full panel		IRS	
Variable	Sum sq %	P-value	Sum sq %	P-value
G_i	99	<0.001	99	<0.001
L_j	0.2	<0.001	0.2	<0.001
$G{:}L_{ij}$	0.4	<0.001	0.4	<0.001
$L{:}R_{jk}$	0.07	<0.001	0.07	<0.001
Residuals	0.5		0.5	

	Cultivars		Experimental lines	
Variable	Sum sq %	P-value	Sum sq %	P-value
G_i	99	<0.001	99	<0.001
L_j	0.04	<0.05	0.4	<0.001
$G{:}L_{ij}$	0.2	<0.01	0.4	0.081
$L{:}R_{jk}$	0.1	<0.01	0.07	<0.05
Residuals	0.4		0.5	

The distribution of mean plant height per group and selection cycle according to Model *f* is visualised in Figure 10. In both locations, the highest mean plant height was observed for cycle 6, with an average of 96 cm in Iceland and 87 cm in Norway. The lowest plant height was observed in the cultivars, with a mean of 84 cm in Iceland and 82 cm in Norway. The Pearson correlation coefficient between locations was r=0.44, and significant ($p<0.05$; Figure 11).

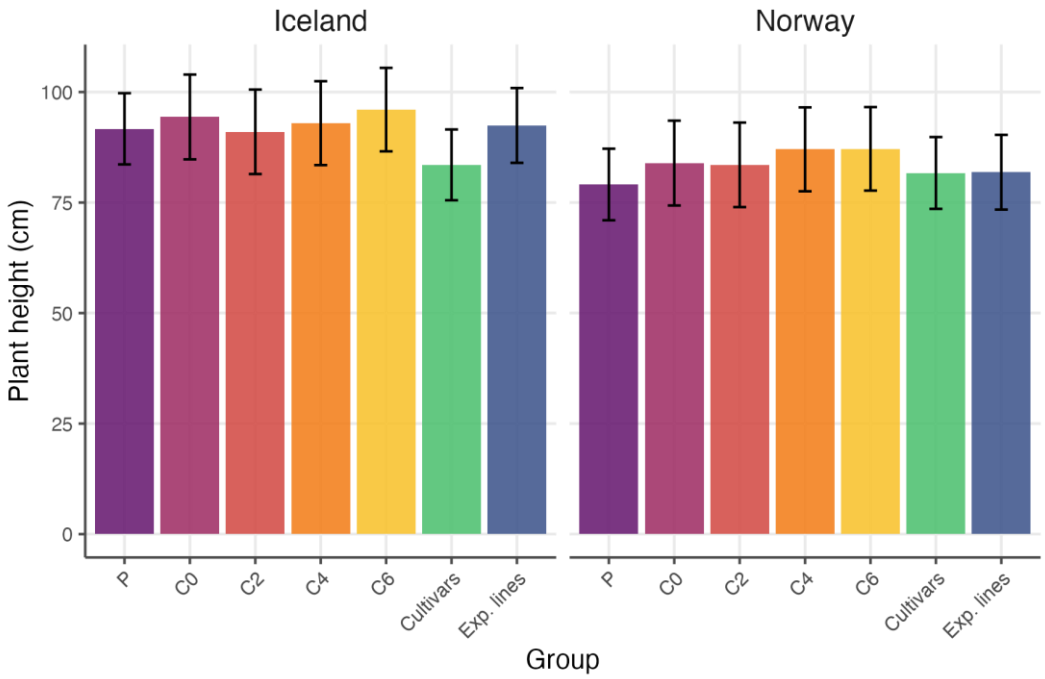

Figure 10. Differences in mean plant height per group and selection cycle in Iceland and Norway, derived from Model f.

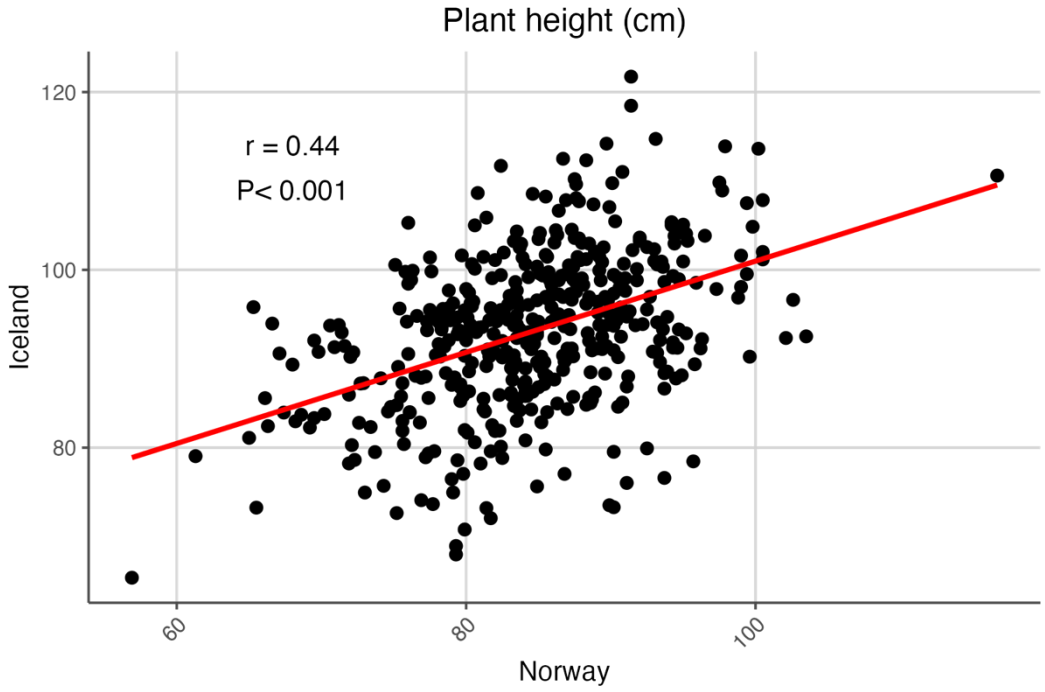

Figure 11. Scatter plot illustrating the significant Pearson correlation coefficient (r=0.44) for plant height (cm) between Iceland and Norway.

As indicated by Model *d*, the observed variance for plant height was 89.72 in Iceland and 18.05 in Norway (Appendix 4). The genetic correlation was estimated at 0.76. H^2 for the full panel was 0.27 across locations, with values of 0.26 in Iceland and 0.65 in Norway. The cultivars exhibited an H^2 of 0.12 across locations, experimental lines 0.45 and the IRS population 0.23.

3.2.4 Lodging

The mean lodging score in Iceland was 64, and in Norway 32 (Figure 12). The observed mean normalized score for Cilla was 39. In Norway, 62 plots showed no signs of lodging. In Iceland, the lowest lodging severity was observed for the experimental line N364-2 with a score of 12. The IRS genotype IA91286 from cycle 0 was the most affected by lodging in Norway while in Iceland, the most affected was IRS genotype IA96407 from cycle 4. Both IA91286 and IA96407 exhibited a normalized lodging score of 100. Within the IRS population in Iceland, 86 genotypes exhibited lower lodging scores than Cilla.

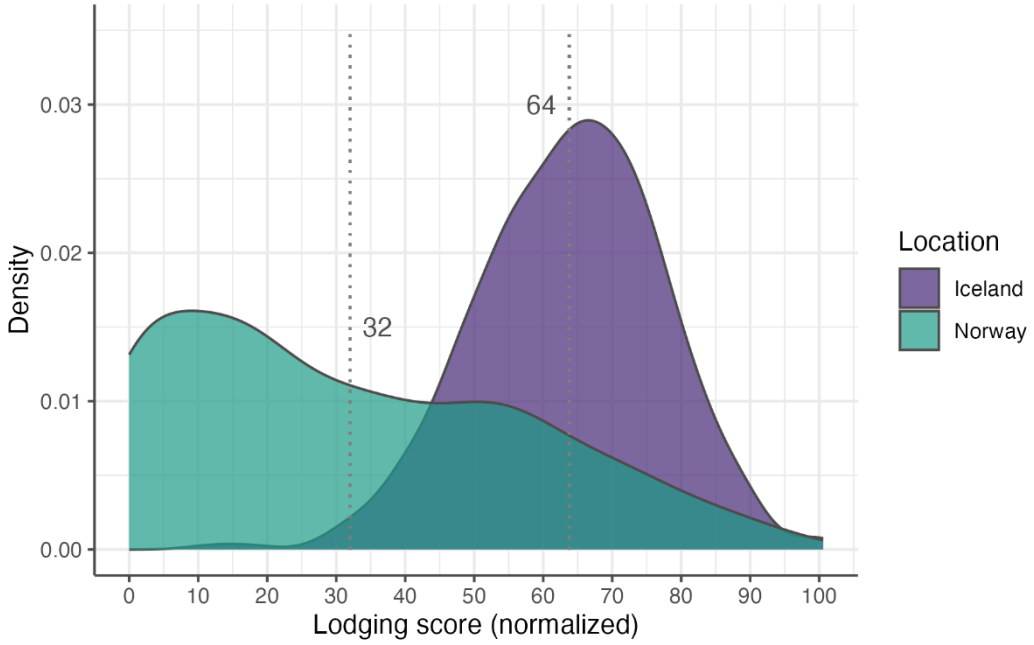

Figure 12. Density plot illustrating the distribution of normalised lodging scores and mean lodging scores in Iceland and Norway.

According to Model *c*, the contribution of the genetic effect of the total SS for lodging was 80% for the full panel and 81% for IRS population (Table 6). The contribution of the genetic effect was 65% for cultivars and 78% for experimental lines. The GxE variable explained between 3-7% of the variation and was significant for all groups except for the cultivars.

Table 6. Fraction of variance in normalized lodging score explained by covariates in Model c. G_i *denotes genotype i grown in location* L_j*, while* $G{:}L_{ij}$ *captures the interaction between genotype i and location j.* R_{jk} *represents the nested effect of replicate k within location j.*

	Full panel		IRS	
Variable	Sum sq %	P-value	Sum sq %	P-value
G_i	80	<0.001	81	<0.001
L_j	7	<0.001	6	<0.001
$G{:}L_{ij}$	7	<0.001	7	<0.001
$L{:}R_{jk}$	0.4	<0.001	0.4	<0.001
Residuals	6		6	

	Cultivars		Experimental lines	
Variable	Sum sq %	P-value	Sum sq %	P-value
G_i	65	<0.001	78	<0.001
L_j	20	<0.001	11	<0.001
$G{:}L_{ij}$	3	0.051	7	<0.01
$L{:}R_{jk}$	4	<0.001	0.1	0.43
Residuals	9		5	

The mean lodging scores per group and selection cycle according to Model *f* is visualised in Figure 13. In Iceland, the highest mean lodging score was observed for the parental lines in the IRS population, with an average score of 69. The lowest observed lodging in Iceland was that of the cultivars, with a score of 57. In Norway, cycle 6 exhibited the highest lodging score of 44, and the lowest was that of the cultivars (6). The Pearson correlation coefficient of lodging between locations was r=0.23, and significant ($p<0.05$; Figure 14).

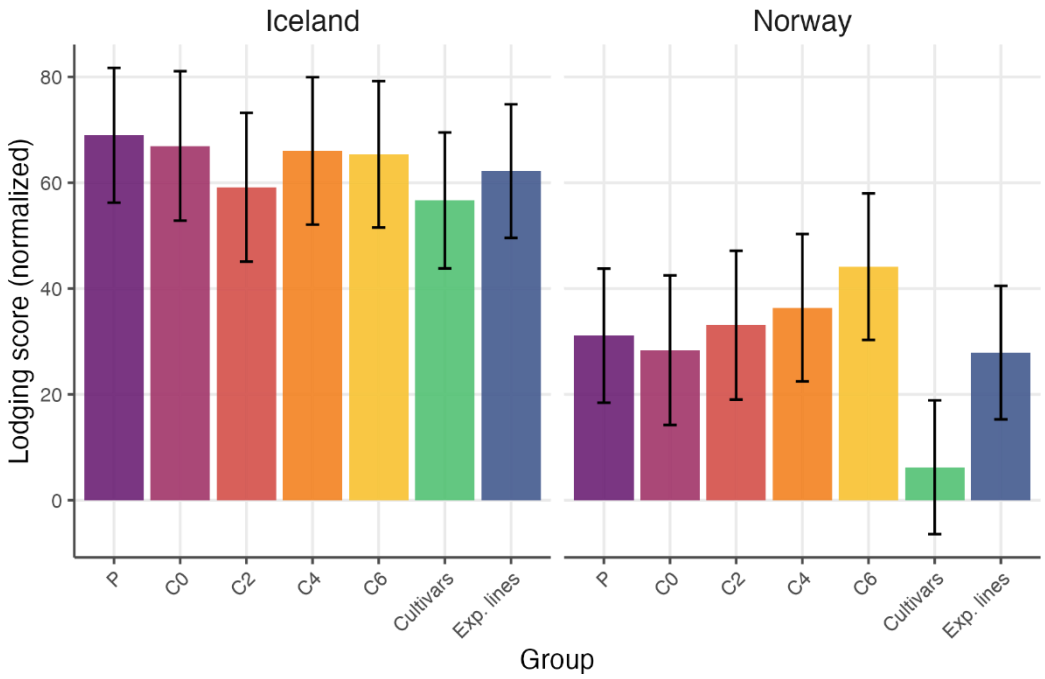

Figure 13. Differences in lodging scores per group and selection cycle in Iceland and Norway, derived from Model f.

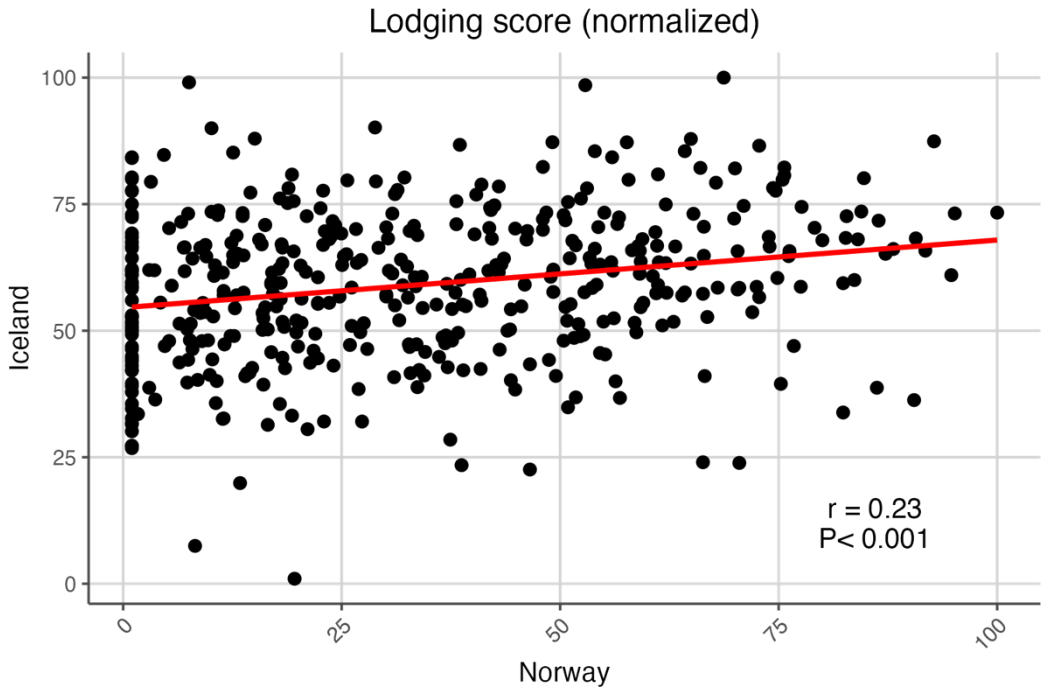

Figure 14. Scatter plot illustrating the significant Pearson correlation coefficient (r = 0.23) for normalized lodging scores between Iceland and Norway.

As indicated by Model *d*, the observed variance in lodging scores was 125.4 in Iceland and 505.4 in Norway (Appendix 4). The genetic correlation was estimated at be 0.3. H^2 for the full panel was 0.21 across locations, with values of 0.16 in Iceland and 0.56 in Norway .The cultivars exhibited an H^2 of 0.00 across locations, experimental lines 0.26 and the IRS population 0.20. Estimations of H^2 for all assessed traits both within and across locations are shown in Table 7. H^2 estimators for the tree groups within the seed panel calculated across locations are shown in Table 8.

Table 7. Broad sense heritability for all traits of the full seed panel estimated across and within each location.

Trait	Across locations	Iceland	Norway
PE	0.69	0.83	0.89
Maturity	0.37	0.51	0.47
Plant height	0.27	0.26	0.65
Lodging	0.21	0.16	0.56

Table 8. Broad sense heritability of all traits and each group within the seed panel, estimated across locations.

Trait	IRS population	Experimental lines	Cultivars
PE	0.69	0.56	0.72
Maturity	0.34	0.30	0.64
Plant height	0.23	0.45	0.12
Lodging	0.20	0.26	0.00

3.2.5 Correlation between traits

A Pearson correlation matrix was computed to examine the pairwise phenotypic correlations among traits characterised in the seed panel (Figure 15). Pearson correlation coefficients were significant across all traits and locations, with the exception of the correlations between plant height and maturity score and lodging score and maturity score in Iceland. Plant height and lodging were positively correlated in both locations and moderately high. The correlation between PE and maturity was negative both across and within locations, with the lower correlation being that in Iceland.

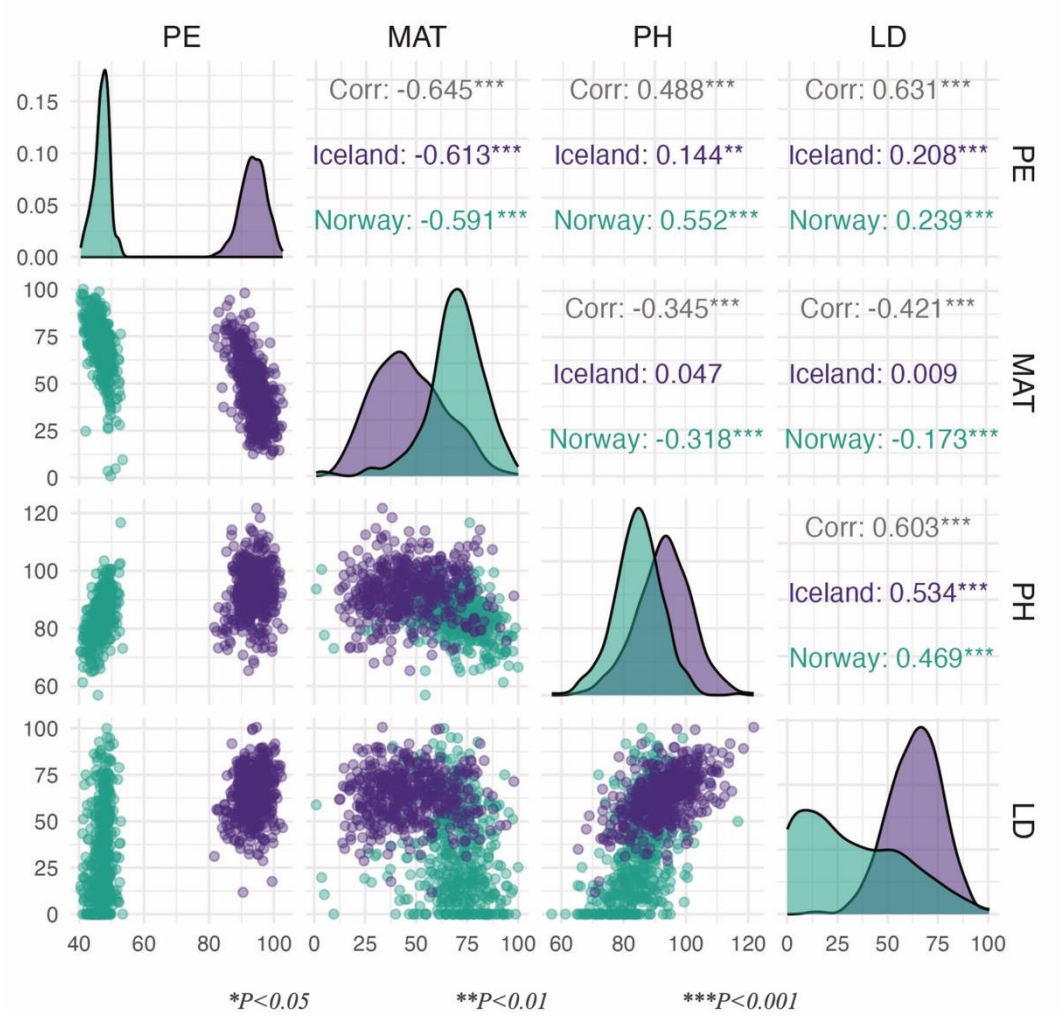

*Figure 15. Pairwise Pearson correlation coefficients between panicle emergence (PE), normalized maturity score (MAT), plant height (PH) and normalized lodging score (LD). The stars indicate significance level with p > 0.05: no star, p < 0.05: *, p < 0.01: **, and p < 0.001: ****

3.3 Association analysis

The data sets provided by NMBU contained genotypic information for 5056 SNPs and 487 seed samples. Of these samples, 445 were present in the phenotypic data derived from Model *b*. 3521 markers were reciprocal in the genotypic data and consensus map, and from these eight monomorphic and three duplicated markers were removed. 271 markers did not pass the threshold of MAF <5% implemented in GAPIT. The final data set used for the association analysis consisted of 3039 high quality polymorphic SNPs.

The first six principal components (PC) included in the association analysis accounted for 22% of the genetic marker variation (Table 9). PC1 accounted for 6.6% of the total variation, and PC2 accounted for 4.8%. A scatterplot of the first two PCs is presented in Figure 16.

Table 9. Eigenvalues and proportions of genotypic variation explained by the first six principal components (PCs) of the principal component analysis. Included are eigenvalues, proportion of total variance accounted for by each PC and the cumulative proportion of variance explained by each PC.

PC	Eigenvalue	Proportion of total	Cumulative proportion
1	141	7%	7%
2	101	5%	11%
3	64	3%	14%
4	60	3%	17%
5	52	2%	20%
6	49	2%	22%

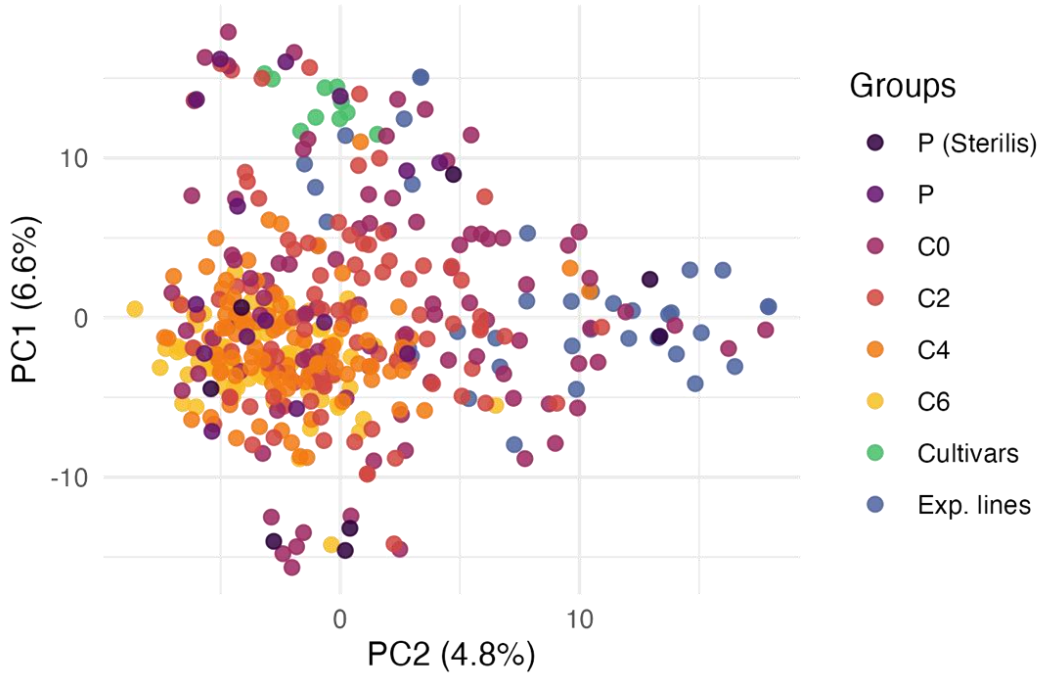

Figure 16. Scatter plot illustrating the distribution of sequenced genotypes from the full seed panel in relation to the first two principal components (PC) from the principal component analysis (PCA).

Table 10 presents the observed mean values for MAF and heterozygosity across all markers. The highest MAF was observed in the cultivars, 32.4%, while the lowest was that of cycle 6, 24.7%. The observed heterozygosity ranged between 7.6% (cultivars) and 9.2% (experimental lines).

Table 10. Minor allele frequency and observed heterozygosity across all SNP markers, divided by group and cycle.

Group/cycle	Minor allele frequency	Observed heterozygosity
P	27.8%	9.0%
C0	27.7%	8.5%
C2	26.6%	8.7%
C4	24.9%	8.4%
C6	24.7%	8.5%
Cultivars	32.4%	7.6%
Exp. lines	31.3%	9.2%

The genome-wide association study (GWAS) identified six individual SNPs that showed significant associations to three traits: PE, maturity score and plant height. SNP markers and positions are listed in Table 11. P-values for all SNPs are visualised in Manhattan plots in Figure 17. The overall strongest association was observed for SNP marker GMI_ES_CC4504_192 on chromosome 7D, with a p-value of 4.68^{-06} (Table 11). This marker was the only one for which significant associations were found for more than one trait. The chromosome assignment follows the nomenclature proposed by Jellen et al. (2024).

Table 11. SNP markers associated to evaluated to panicle emergence (PE), maturity score (MAT), plant height (PH) and positions of markers.

Trait	SNP marker	Chr.	Pos. (cM)	P-value	MAF
PE	ZOT004030	4C	54.2	4.68^{-06}	0,05
	GMI_ES15_c16835_340	4C	63.9	1.59^{-06}	0,30
	GMI_ES_CC4504_192	7D	60.2	8.09^{-14}	0.14
MAT	GMI_ES_CC4504_192	7D	60.2	9.67^{-11}	0.14
	GMI_ES03_c3849_1052	7C	68.3	1.36^{-07}	0,20
PH	ZOT002086	3A	92.1	1.76^{-07}	0,25
	GMI_ES02_c840_525	4A	78.1	3.91^{-06}	0,33

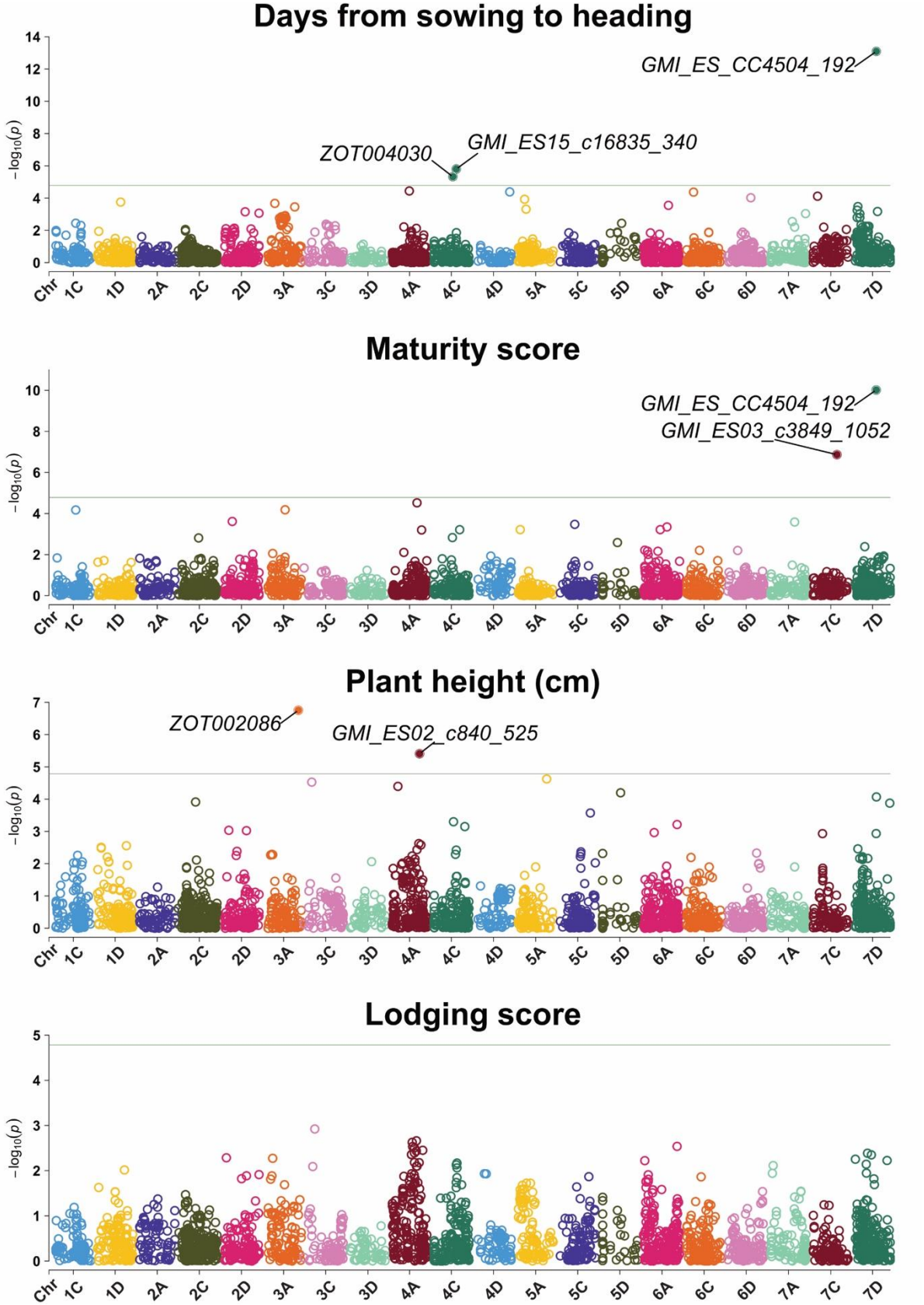

Figure 17. Manhattan plots showing markers with significant hits for panicle emergence, maturity and plant height. The green line signifies the Bonferroni corrected threshold.

In Figure 18, minor allele frequencies at loci for SNPs with significant marker-trait associations are visualised, divided by cycle of selection in the IRS population. Corresponding frequencies for the cultivars, experimental lines and the full IRS-panel are presented in Figure 19.

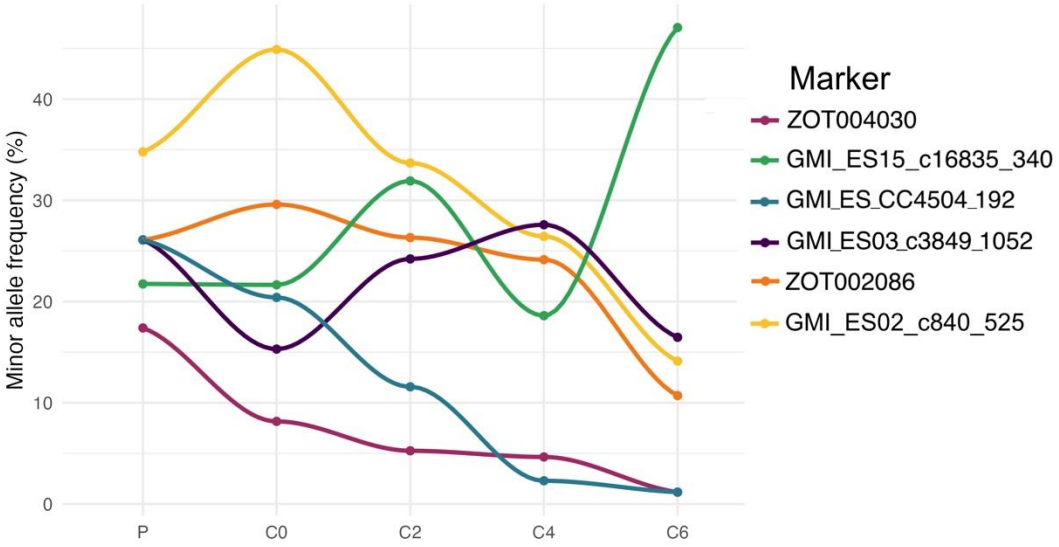

Figure 18. Minor allele frequencies for each identified significant marker-trait association, divided by cycle of selection in the IRS-material.

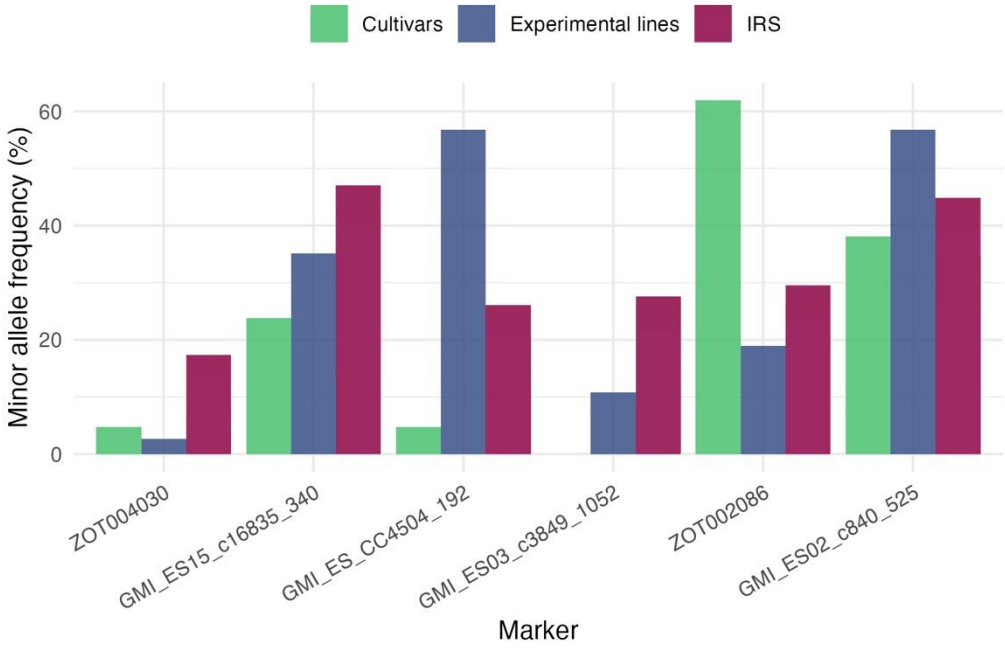

Figure 19. Minor allele frequency per group in the seed panel, for each significant SNP identified in the association analysis.

In Figure 20, the relationship between the presence of minor allele “C” at the GMI_ES_CC4504_192 loci and mean values for PE and maturity score is visualised. Plots visualising the relationship between the other significant markers and corresponding traits are presented in Appendix 5. Presence of the minor allele at the GMI_ES_CC4504_192 loci per selection cycle and group is presented in Table 12. Among the parental lines, the minor allele was only found in genotypes with *A. sterilis* introgression, with the exception of it being present in the parental lines Newman and the daylight-insensitive AC Lotta (Table 13). Additionally, for three parental lines with *A. sterilis* introgression the major allele "T" was present the GMI_ES_CC4504_192 locus, along with the remaining parental lines.

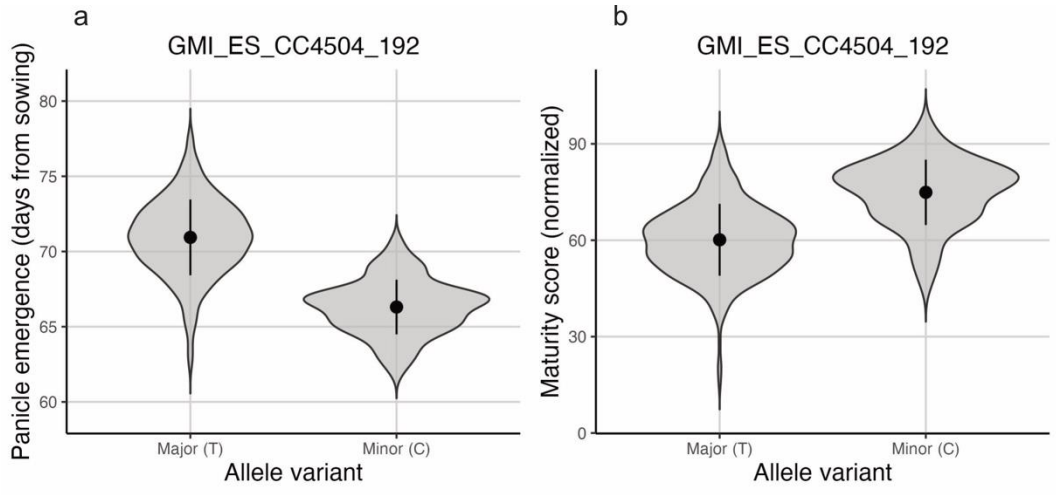

Figure 20. Violin plots visualizing the relationship between the allele variant present at the GMI_ES_CC4504_192 loci and a) mean panicle emergence (PE) b) mean normalized maturity score.

Table 12. Proportion of genotypes per group and cycle with the minor allele “C” present at the GMI_ES_CC4504_192 loci.

Group	MAF
Parental lines	26%
C0, IRS population	21%
C2, IRS population	12%
C4, IRS population	2%
C6, IRS population	1%
Experimental lines	43%
Cultivars	0%

Table 13. Allele variant present at the GMI_ES_CC4504_192 loci in parental lines of the IRS population.

Parental line	Allele (T/C)	Characteristics
A80004-2	T	
A80004-2	T	
A80004-2	T	
B605X	T	
D921-643	T	*A. sterilis* introgression
Don	T	
Frigg	T	
H61-3-3	T	
H688-4	T	
Lena	T	
Martin	T	
Munin	T	
Ogle	T	
Premiere	T	
Premiere	T	
Z595-7	T	*A. sterilis* introgression
Z615-4	T	*A. sterilis* introgression
Newman	C	
Sheldon	C	*A. sterilis* introgression
Z519-4	C	*A. sterilis* introgression
Z537-2	C	*A. sterilis* introgression
Z562-3	C	*A. sterilis* introgression
AC Lotta	C	Hull-less, daylength insensitive

4. Discussion

4.1 Population structure

A PCA was conducted to determine whether any population structure was present in the seed panel. The analysis revealed that the first six PCs accounted for only 22% of the genetic variation, indicating no strong population structure present in the material (Table 9, Figure 16). If a strong population structure had been present, it could potentially have entailed false associations or reduced detection power, and the lack of strong population structure in the material is therefore an indication of reliable results from the GWAS. Similar observations of weak or no populations structure have been reported in for diverse oat panels in previous studies. (Newell et al. 2011, 2012; Esvelt Klos et al. 2016; Huang et al. 2020). Furthermore, the studies report geographic origin or binary morphological traits such as lemma colour are the largest contributing factors to the presence of population structure in oat panels. The seed panel in this study consisted of recurrent selection material with parental lines originating from North America and Scandinavia and thus, no clustering based on geographical origin is to be expected. The commercial and experimental lines included in the panel formed separate clusters (Figure 16), but these clusters were all to some extent overlapped by IRS genotypes. The tight clustering of the cultivars is in line with the previously reported narrow diversity of the Nordic oat gene pool (Grau Nersting et al. 2006; Achleitner et al. 2008; Tinker et al. 2009).

Overall, the results indicate that the IRS population possesses a larger genetic diversity compared to the cultivars and experimental lines. This is promising in the context of using the IRS population as pre-breeding material for oats adapted to Icelandic conditions.

4.2 Panicle emergence and maturity

The observed H^2 of PE in the extreme environment of Iceland was high (0.83), and in Norway even higher (0.89; Table 7). This indicates that the trial designs were able to account for spatial variations and that the experiment was successful. The high heritability of PE is in line with previous reports on the heritability of phenology-related traits. For instance, in similar studies on oats Leišová-Svobodová et al. (2019) reported a H^2 of 0.94 for PE and Buerstmayr et al. (2007) 0.92.

Observed H^2 for PE was lower across than within locations (Table 7). However, the genetic effect was estimated at 90% (Table 3), which together with the moderately high Pearson correlation coefficient (Figure 5) indicates that expression of PE was generally stable across locations. This is further supported by the genetic correlation of 0.84 between locations suggested by Model *d* (Appendix 4).

The timing of PE is mainly dependent on temperature and photoperiod (Trevaskis et al. 2022), and the suboptimal conditions in Iceland were expected to have a large impact on the trait. The results confirmed this, since PE occurred later and spanned a longer period of time in Iceland compared to Norway where the climate is milder (Figure 3). The mean PE in Iceland occurred 94 days after sowing, nearly twice as late as the mean PE of 47 days in Norway. Further, the difference in ATS between the first day of PE in Iceland and first panicle in Norway was 163° (Figure 2). The longer photoperiod in Iceland appears to affect the timing of PE, as the difference between locations cannot be attributed only to variations in ATS. Trevaskis et al. (2022) found that the acceleration of PE due to an extended photoperiod reaches a maximum at >18h, and that longer period does not increase developmental rate. In Norway, the photoperiod peaked at ~18h while in Iceland at ~21.5h (Figure 2). Therefore, the development rate in Iceland is likely affected by the longer photoperiod before its peak, but it seems that ATS remains the limiting factor for an accelerated development. However, during the first half of the growing season, Iceland the precipitation in Iceland was heavy. This may have resulted in fewer hours of sunlight compared to Norway during this period, making it difficult to draw certain conclusions about the effect of the photoperiod on development.

For maturity, H^2 estimations were considerably lower than those of PE (Table 7). This indicates that maturity as a trait is more sensitive to environmental effects or that differences in phenology become more apparent in later development stages. The Icelandic trial displayed a higher H^2 for maturity (0.51) than in Norway (0.47). Both these observations are lower than the H^2 of 0.81 for days to maturity reported by Leišová-Svobodová et al. (2019). Among all traits, the difference in genetic variation between locations was the highest for maturity (Appendix 4). Supporting

this is that the Pearson correlation coefficient was lower for maturity than for PE, suggesting GxE to have a larger effect on maturity (Figure 5 & 8). This was further supported by a larger fraction of the total SS being attributed to the GxE variable for maturity than for PE (Table 3, Table 4). However, these factors were of little magnitude and represented small fractions of the total phenotypic variance, which indicates a low degree of GxE affecting maturity, contradicting the results from Model *c* and the Pearson correlation coefficient.

The minimum GxE interaction for both maturity and PE reported here is in line with a study on wheat by Ochagavía (2019). Ochagavía's study aimed to quantify *Esp* by temperature interactions under different temperature conditions, comparing results from trials in Spain and in the UK. Genotypes carrying the *Esp* early allele demonstrated early heading regardless of temperature, but the magnitude in difference between late and early genotypes were larger in cooler climates. Further, no cross-over effect in phenotypic expression was observed between trial locations. These results agree with the observed response of PE and maturity score in this study, where results from Model *d* indicate greater phenotypic variance for both traits in Iceland (Appendix 4).

The observed PE is not important for cultivation per se but is often used as an indicator of the expected time required for the genotype to reach maturation. The observed correlation between PE and maturity score in this study were only moderately high, although almost equal in Iceland and Norway (Figure 15). The observed H^2 was higher for PE than for maturity (Table 7), and a perfect correlation is therefore not expected, since both traits are influenced by environmental factors to varying degrees.

The strongest marker-trait association found in this study was that for marker GMI_ES_CC4504_192 on chromosome 7D, which was found to be associated with both PE and maturity (Table 11, Figure 17). The genomic region where this marker is positioned has in previous studies been identified to contain QTLs for time to PE (Esvelt Klos et al. 2016; Bekele et al. 2018; Zimmer et al. 2018; Huang et al. 2020; Tinker et al. 2022). Furthermore, the position of GMI_ES_CC4504_192 is according to Tinker et al. (2022) flanking the position of the vernalisation responsive gene *Vrn3*. Tinker proposes *Vrn3* on chromosome 7D to be the *Vrn* homologue with the most significant effect on time to PE. GMI_ES_CC4504_192 could potentially co-localize with the previously mentioned QTLs and *Vrn* homologue, but it is not possible to determine whether this is due to pleiotropy or genetic linkage. As seen in Figure 20, the presence of the minor allele "C" corresponded with both earlier PE and increased maturity score. This allele variant was absent among the cultivars and less frequent in later selection cycles compared to early in the IRS population (Figure 18 & 19). Among the parental lines, the minor

allele was more common in parental genotypes with *A. sterilis* introgression. Since the early "C" allele is absent among the Nordics cultivars, there are opportunities to create earlier material through introgression using marker-assisted selection.

In proximity to the previously mentioned QTLs on chromosome 7D, several QTLs for plant height have been identified (Tinker et al. 2022) as well as a cluster of rust resistance genes (Esvelt Klos et al. 2017; Sunstrum et al. 2019). According to Bekele et al. (2018), such co-occurrence of QTLs together with a proven reduced recombination on this end of 7D points towards a selective sweep having influenced the region. Similar effects have been found in other cereals where heavy selection and breeding has resulted in a decreased haplotype diversity, especially in regions of heading and maturity related genes. Such regions of low haplotype diversity can cause problems when breeders want to separate closely located regions affecting different traits (Tinker et al. 2022).

Marker GMI_ES15_c16835_340, located on chromosome 4C, was found to be associated with PE (Table 11, Figure 17). This marker is located only 1000 bp upstream of a marker positioned within a QTL suggested to be associated with increased frost tolerance (Tumino et al. 2016). In proximity to GMI_ES15_c16835_340 on chromosome 4C is marker ZOT004030, found here to associate with PE (Table 11, Figure 17). However, this marker does not appear to coincide with the QTL for frost tolerance identified by Tumino et al. (2016).

A marker-trait association was found between marker GMI_ES03_c3849_1052 and maturity score (Table 11, Figure 17). Near the marker's location on chromosome 7C is a QTL associated to plant height, identified by Zimmer et al. (2018). In other cereals such as wheat plant height, PE and yield related traits are often inter-related and share common QTL complexes (Martinez et al. 2021). Therefore, it is possible that marker GMI_ES03_c3849_1052 is located within or shares a common complex with the QTL identified by Zimmer et al. (2018). Even though not flanking, a putative *Vrn1* homologue (Tinker et al. 2022) is located in proximity and potentially co-localized to GMI_ES03_c3849_1052.

4.3 Plant height and lodging

The broad sense heritability for plant height across locations was unexpectedly low, only 0.27 (Table 7). The heritability for plant height in wheat is often found to be high, and observations has in previous studies ranged between 0.85 and 0.96 (Schneider et al. 2024; Singh et al. 2024; Zewdu et al. 2024). In studies on conducted on oats, heritability observations considerably higher than those in this

study have been reported, ranging between 0.73 and 0.96 (Buerstmayr et al. 2007; Leišová-Svobodová et al. 2019; Ranjan et al. 2024).

The H^2 for plant height observed in Iceland was lower than that that of Norway, potentially due to heavy rainfalls in May and June in Iceland (Table 7). The large amount of precipitation led to waterlogging in parts of the trial field. Waterlogging can cause major negative effects on plant development, since saturated conditions lead to anaerobic environments for roots, which in turn prevents proper turnover and mineralization of organic compounds (Manghwar et al. 2024). Signs of nutrient deficiency, such as stunted growth, chlorosis and lankiness in plants were observed in affected areas of the trial. It is likely that the waterlogging caused stunted vegetative growth in saturated parts, and the lower H^2 of plant height observed in Iceland may be due to these spatial variations not being fully accounted for by the model.

According to Model *d*, the genetic correlation for plant height between locations was moderately high (0.76; Appendix 4). The genetic effect of the total SS was estimated at 99% for the full panel, and the effect of the GxE variable was small, however still significant (Table 5). Overall, this suggests stable performance in plant height across locations. Contradicting this proposed stability is the rather low Pearson correlation coefficient between locations (Figure 11). However, the presence of outliers in Figure 11 may have influenced this result, leading to a reduced correlation.

For lodging, H^2 was moderately high in Norway, but low in Iceland and across locations (Table 7). The large difference in heritability between locations may be attributed to the large number of plots in Iceland experiencing severe lodging due to heavy winds. Mathias-Ramwell et al. (2023) observed that H^2 for lodging expressed in percentage of plants lodging was almost twice as high as H^2 for assessment of lodging severity. This could partly explain why the observed H^2 in Norway was higher, where lodging was assessed by estimating only the percentage of plants affected by lodging. The Norwegian scoring index did not account for the severity of lodging, a factor which was integrated in the Icelandic scoring index. As demonstrated by Model d (Appendix 4), the genetic variance for lodging was considerably larger in Norway than in Iceland. Furthermore, the extreme degree of lodging in Iceland may have reduced phenotypic variation, resulting in a deflated H^2 which could, in turn, explain why no marker-trait associations were found for this trait. QQ-plots (Appendix 1) indicate underfitting of the GWAS model for the lodging trait. Performing additional model evaluations by adjusting the number of PCs used as covariates for each trait individually could potentially reveal significant marker associations for lodging.

The significant impact of the environment on lodging occurrence was further supported by the low genetic correlation according to Model *d* (Appendix 4). According to Model *c*, the genetic effects accounted for 80% of the total SS. Both these observations were lower than those of the other studied traits. Additionally, of all traits lodging demonstrated the lowest Pearson correlation coefficient between locations, although still significant (Figure 14). All Pearson correlation coefficients between traits were found to be significant in this study, except for two correlations in Iceland (Figure 15). In Iceland, the correlation between maturity and plant height was not significant, neither was that between maturity and lodging. The observed H^2 for plant height and lodging in Iceland were low (Table 7), which agrees with the non-significant Pearson correlations, further supporting the previously mentioned assumption that phenology related traits are less prone to GxE.

The Pearson correlation coefficient for plant height and lodging was moderately high in both locations, with r = 0.47 in Iceland, and r = 0.60 in Norway (Figure 15). This is in agreement with correlations ranging between 0.29 - 0.62 observed in similar studies (Buerstmayr et al. 2007; Boczkowska et al. 2016; Mathias-Ramwell et al. 2023). Traits such as stem width and straw strength are known to impact lodging susceptibility (Marshall 1992), and a perfect correlation between plant height and lodging is therefore not expected. In Norway, the parental lines demonstrated a lower plant height than the cultivars (Figure 10), but the cultivars proved far more resilient to lodging even though taller (Figure 13), confirming that other factors affect lodging susceptibility. Therefore, while the moderately high Pearson correlation suggests that plant height needs to be considered when selecting for lodging resistance, the inclusion of additional traits such as stem strength and width might allow for a more precise analysis.

In the association analysis, two marker-trait associations were found for plant height. One of these associations was that of marker ZOT002086 (Table 11, Figure 17). According to the consensus map provided by NMBU which was used for marker positioning indicates that ZOT002086 is positioned on chromosome 3A. In contrast, the developers of the SNP chip used for genotyping suggest the marker to be located on chromosome 1C (Polley et al. 2023). The proposed position on chromosome 1C overlaps with previously identified QTLs associated with root growth rate (Huang 2020) and plant height (Sunstrum et al. 2019). The presence of the minor allele “A” at the ZOT002086 loci appears to have a negative impact on plant height (Figure 20). Marker ZOT002086 is the only identified significant marker for which the cultivars demonstrated the highest MAF of all groups (Figure 19). This high MAF agrees with the minor allele’s effect on plant height, as reflected in the low mean height of this group (Figure 10). In this study, the designation of the minor allele was determined based on its frequency within the

seed panel instead of assigning the minor allele based on the variant present at the loci according to a reference or pan-genome. The highest overall MAF was observed among the cultivars, suggesting that some assigned major alleles may actually be the true variant alleles relative to the pan-genome. Further analysis including a reference genome could provide additional insight into this.

The second marker-trait association for plant height was that with marker GMI_ES02_C840_525 on chromosome 4A (Table 11, Figure 17). QTLs for plant height have been identified upstream of GMI_ES02_C840_525 by Zimmer et al. (2018) and He et al. (2013). Moreover, located on the same end of chromosome 4A is a proposed homologue of *Vrn1* (Tinker et al. 2022) but further studies evaluating potential co-localizations in this region are needed.

4.4 Comparison between groups

According to Model *c*, the cultivars demonstrated lower GxE for PE, maturity and lodging compared to the other groups (Table 3, 6 and 9). According to model d, the cultivars exhibit larger genetic correlation for PE and maturity score compared to the IRS population (Appendix 4). This suggests a more uniform performance of the cultivars across locations, which is further supported by the high H^2 for PE and maturity observed in this group (Table 7). However, the small sample size of the cultivars compared to the large, heterogenous IRS population makes drawing conclusions about differences in performance difficult.

Cilla was chosen as a check for the Icelandic trial due to its previous successful cultivation in Iceland. In all evaluated traits, Cilla exceeded the performance of the full panel. As this study seeks to evaluate IRS population's potential as pre-breeding material and to identify promising germplasm sources, it is not expected that the IRS population would outperform the cultivars. For each trait, several IRS genotypes surpassed Cilla's performance but continued research focusing on these individuals is needed for further selection.

4.5 Development over cycles

Previous studies have proposed grain number to be the determining factor of grain yield amount in oats (Peltonen-Sainio 1991; Peltonen-Sainio et al. 2007; Howarth et al. 2021). This is argued to be a due to a longer stem elongation phase allowing for the formation of more fertile florets per panicle, resulting in an increased number of grains. As a result, breeding efforts focusing on increasing yield could potentially entail later PE if the pre-anthesis phases are prolonged. In a study

comparing Nordic landraces to old and modern cultivars, Grau Nersting et al. (2006) did not observe this effect. Instead, the modern cultivars demonstrated earlier PE than low-yielding landraces and old cultivars. Similarly, in a study conducted on Finnish cultivars released between 1921 and 1988, Peltonen-Sainio and Rajala (2007) found no correlation between a prolonged stem elongation phase and grain yield. Instead, only the duration of the grain filling appeared to have been altered by breeding. Along with the overall growing time, the duration of grain filling was shortened, while the period leading up to anthesis remained unchanged. The limiting factor for successful oat production in the Nordic countries is the naturally short growing season. It is possible that Nordic breeding has increased the yield potential by other mechanisms than a prolonged stem elongation phase, in order to conserve early PE dates.

A trend of delayed PE over selection cycles was observed in this study (Figure 4). Similarly, maturity scores appeared to decrease in later cycles (Figure 7), corresponding to negative correlation between PE and maturity (Figure 15). The trend of later PE over selection cycles in the IRS population was observed by Holland et al. (2002). This change was however of small magnitude, with PE being delayed only 0.1 days per cycle. The effect was considered significant in the two northernmost trial locations but not in a trial of a latitude further south. The IRS material was developed to enhance yield and improve dynamic stability, and the delay in PE over cycles could potentially be an effect of a prolonged stem elongation phase resulting in an increased number of grains. One indication of this is the positive correlation between PE and plant height (Figure 15) together with what appears to be an increase in plant height over cycles (Figure 10). Buerstmayr et al. (2007) and Boczkowska et al. (2016) found plant height to be negatively correlated to yield, contradicting the possible connection between increased yield and a prolonged stem elongation phase. The mechanism underlying the yield increase observed by Holland et al. (2000) is not known. Whether the negative correlation between height and yield proposed by Buerstmayr et al. (2007) and Boczkowska et al. (2016) applies to the IRS-material under extreme Icelandic conditions remains uncertain.

According to PCA-analysis (Figure 15), the genetic diversity among parental lines and early cycles of selection was the largest of all group, possibly due to the *A. sterilis* introgression. The diversity did, however, appear to decrease over cycles of selection. Similarly, a trend of decreased MAF and observed heterozygosity over cycles of selection within the IRS-material was observed (Table 10). Holland et al. (2000) demonstrated a high genetic gain over cycles in the IRS population when breeding for increased yields. A tapered genetic diversity is expected to follow as a result of response to selection (Oldenbroek & van der Waaij 2014). Therefore, the later cycles of selection might not be suitable for further pre-breeding, since alleles

responsible for earliness and short plant height may be lost. However, the diversity in C6 still appears larger than that of the cultivars, and the great dispersal of IRS-material in the Figure 15 proves that introgression of *A. sterilis* and American cultivars has entailed a richness of allelic variation. This variation could contribute to a broadening of the currently narrow Nordic oat gene pool.

4.6 Conclusions

Despite harsh conditions in Iceland such as heavy precipitation and high weed pressure, the majority of genotypes demonstrated great vigour and resilience. The high H^2 for plant height and PE proves that the trials were relatively successful, as the trial design were able to account for a large amount of the non-genotypic variation. A storm in early September caused extensive lodging in the Icelandic trial, and at the time for harvest most plots were lodging. Since the aim of this study was to evaluate the material's performance in a suboptimal environment, challenging conditions such as heavy rain and winds are not obstacles but should instead be considered as as crucial factors for proper analysis.

PE was the trait least affected by GxE, although all traits demonstrated minimal GxE impact. This uniform behaviour agrees with the high dynamic stability reported by Holland et al. (2000). However, for all traits except maturity, H^2 observations were lower in Iceland than in Norway. This suggests that the extreme Icelandic environment has a great influence on trait expression, resulting in increased phenotypic variation. The differences in H^2 between locations, together with the low H^2 across locations, indicates that a domestic breeding program is necessary for adapting oats to Icelandic conditions, as the extreme environment significantly impacts the otherwise stable IRS population. While earliness is the most crucial trait when developing oats adapted to Iceland, yield potential also needs to be considered for production to be profitable. Further trials in coming years will reveal whether the increased yield stability over cycles reported by Holland at al. (2000) will manifest under suboptimal conditions.

The purpose of this study was to evaluate whether the IRS population harboured enough genetic diversity and sufficient variation in trait expression to be suitable for further pre-breeding. The IRS population, and especially early cycles, demonstrated large variation in all studied traits, highlighting the material's potential for substantial genetic gain through further selection. Despite the observed delay in PE and increased plant height over selection cycles, several genotypes from earlier cycles were on par with or even surpassed the performance of check cultivar Cilla. The presence of genotypes that outperformed Cilla suggests that the material

contains valuable genetic resources that could provide a solid foundation for future breeding of stable and early oats.

In this study, several significant marker-trait associations were identified and will serve as valuable tools for further breeding efforts aimed at developing oats adapted to extreme and challenging environments. Although later selection cycles of the markers identified in this study, together with the harsh environment's ability to force phenotypic variations to unfold, creates substantial potential for Iceland to emerge frontrunners in the breeding of robust and vigorous oats.

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Popular science summary

In recent years, a large demand for oats among consumers as well as producers has surfaced due to the cereal's health benefits and suitability as an ingredient in plant-based alternatives to meat and dairy products. In Iceland there is no domestic large-scale production of oats today, even though the demand is high. The main reason for this is the lack of suitable cultivars that can withstand the harsh weather conditions, and which mature within the growing season. To ensure oat production in Iceland, new robust varieties with early heading are needed. This study aimed to evaluate the performance of the Iowa Recurrent Selection population (IRS), a pre-breeding material developed for increased yield and uniform performance under varying conditions.

A seed panel was created consisting of IRS genotypes representing four cycles of selections together with elite lines and Nordic cultivars available on the market. To enable comparison of performance across locations, data was collected in field trials conducted in Iceland and Norway. Traits including time to panicle emergence, degree of maturity, plant height and degree of lodging was recorded and analysed through mixed linear modelling. Additionally, a genome-wide association study (GWAS) was carried out seeking to identify genetic markers associated with the studied traits.

Results indicated that the dynamic stability previously demonstrated in the material was not sufficient to ensure minimal environmental effects on trait expression under extreme conditions. An Icelandic domestic breeding programme is therefore necessary for further selection. Several genotypes within the IRS material demonstrated earlier heading and less lodging susceptibility than the control group. Furthermore, the genetic diversity in the population was higher than that of the control group. In the GWAS analysis, six individual markers were found to associate with three of the investigated traits. The presence of genotypes superior to the control group and the large genetic diversity speaks for the suitability of this material's potential as pre-breeding material for oats adapted to Icelandic conditions. Together with the markers identified in the study, there is great potential for this material to constitute a basis for further breeding of early oats in Iceland.

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Appendix 1

List of genotypes included in the seed panel evaluated in the field trial carried out in Iceland are presented in. Through previous evaluations at NMBU, single panicles from individual plants within families that were considered heterogenous were chosen to be evaluated separately. Column “Pan” refers to the number of panicles chosen from each family considered to be heterogenous. Experimental lines are referred to as “Exp.” and cultivars as “Cult.”.

Group	Cycle	Genotype	Pan.	Genotype	Pan.	Genotype	Pan.
IRS	P	A80004-2	3	H688-4		SHELDON	
		AC Lotta		LENA		Z519-4	
		B605X		MARTIN		Z537-2	
		D921-643		MUNIN		Z562-3	
		DON		NEWMAN		Z595-7	
		FRIGG		OGLE		Z615-4	
		H61-3-3		PREMIER	2		
IRS	C0	IA91121		IA91178		IA91252	
		IA91123		IA91180		IA91255	
		IA91126		IA91187		IA91256	
		IA91127		IA91188		IA91262	
		IA91130		IA91190		IA91263	
		IA91135		IA91191		IA91264	
		IA91141		IA91192		IA91266	
		IA91143		IA91193		IA91267	
		IA91144		IA91194	2	IA91268	
		IA91145		IA91196		IA91270	
		IA91146		IA91198		IA91275	
		IA91147		IA91200		IA91278	
		IA91148		IA91202		IA91281	
		IA91149	2	IA91204		IA91282	2
		IA91151		IA91205	4	IA91283	
		IA91154		IA91207		IA91284	
		IA91156		IA91208		IA91286	
		IA91157		IA91209		IA91287	

Group	Cycle	Genotype	Pan.	Genotype	Pan.	Genotype	Pan.
		IA91158		IA91211		IA91288	
		IA91161		IA91215		IA91289	
		IA91162		IA91218		IA91293	
		IA91164		IA91222	2	IA91297	
		IA91167		IA91224		IA91300	
		IA91169		IA91226	2	IA91302	2
		IA91170		IA91227		IA91303	2
		IA91171	2	IA91228		IA91306	
		IA91172		IA91232		IA91307	2
		IA91173		IA91234		IA91309	
		IA91176		IA91238			
		IA91177		IA91246			
IRS	C2	IA93201		IA93263		IA93326	
		IA93203		IA93268		IA93328	
		IA93207	2	IA93273	2	IA93331	
		IA93208		IA93275		IA93335	
		IA93212		IA93276		IA93338	
		IA93213		IA93279		IA93339	
		IA93214		IA93281		IA93341	
		IA93216	2	IA93284		IA93347	
		IA93218	2	IA93286		IA93349	
		IA93219		IA93287		IA93352	
		IA93221		IA93288		IA93353	
		IA93223		IA93290		IA93355	
		IA93227		IA93294		IA93356	
		IA93229		IA93295		IA93364	
		IA93230		IA93298		IA93365	
		IA93234		IA93299		IA93366	
		IA93235		IA93300		IA93369	
		IA93238		IA93301		IA93371	
		IA93239	2	IA93303		IA93372	
		IA93242		IA93304		IA93374	
		IA93244	2	IA93308		IA93377	
		IA93246		IA93310		IA93379	
		IA93247		IA93311	2	IA93381	
		IA93249		IA93313		IA93382	
		IA93250		IA93317		IA93389	
		IA93251		IA93318		IA93390	
		IA93252		IA93319		IA93391	
		IA93254		IA93320		IA93395	

Group	Cycle	Genotype	Pan.	Genotype	Pan.	Genotype	Pan.
IRS	C2	IA93259		IA93322		IA93397	
		IA93260		IA93324			
IRS	C4	IA96204		IA96281		IA96361	
		IA96205		IA96282		IA96362	
		IA96206		IA96283		IA96363	
		IA96208		IA96284		IA96365	
		IA96210		IA96293		IA96366	
		IA96211		IA96294	2	IA96368	
		IA96219		IA96297		IA96369	
		IA96220		IA96298		IA96373	
		IA96221		IA96299		IA96374	
		IA96222		IA96303		IA96375	
		IA96224		IA96307		IA96376	
		IA96228		IA96310		IA96377	
		IA96229		IA96314		IA96379	
		IA96231		IA96315		IA96380	
		IA96234		IA96317		IA96382	
		IA96241		IA96320		IA96385	
		IA96243		IA96323		IA96386	
		IA96246		IA96326		IA96388	
		IA96247		IA96328		IA96394	
		IA96248		IA96330		IA96396	
		IA96251		IA96332		IA96397	
		IA96252		IA96335		IA96398	
		IA96257		IA96339		IA96400	
		IA96260		IA96341		IA96406	
		IA96264		IA96343		IA96407	
		IA96265		IA96346		IA96409	2
		IA96269		IA96349		IA96411	
		IA96270		IA96355		IA96412	
		IA96273		IA96357			
		IA96277		IA96360			
IRS	C6	IA98501		IA98576		IA98638	
		IA98510		IA98577		IA98639	
		IA98514		IA98578		IA98644	
		IA98520		IA98579		IA98645	2
		IA98521		IA98581		IA98646	
		IA98522		IA98585		IA98647	
		IA98527		IA98587		IA98648	
		IA98528		IA98589		IA98649	

Group	Cycle	Genotype	Pan.	Genotype	Pan.	Genotype
		IA98529		IA98591		IA98656
		IA98530		IA98595		IA98663
		IA98536		IA98597		IA98664
		IA98537		IA98598		IA98665
		IA98538		IA98599		IA98667
		IA98539		IA98600		IA98669
		IA98544		IA98602		IA98670
		IA98546		IA98605		IA98678
		IA98547		IA98607		IA98679
		IA98549		IA98608		IA98680
		IA98551		IA98609		IA98681
		IA98552		IA98615		IA98687
		IA98556		IA98616		IA98688
		IA98557		IA98620		IA98689
		IA98560		IA98621		IA98691
		IA98562		IA98629		IA98694
		IA98563		IA98630		IA98695
		IA98564		IA98632		IA98696
		IA98565		IA98633		IA98700
		IA98571		IA98634		IA98701
		IA98573		IA98636		IA98702
Cult.		Belinda		Mo		Romedal
		Cilla		Odal		Våler
		Eidskog		Ridabu		Vinger
		Haga		Ringsaker		
Exp. lines		CI9268		J-75		Y647-9-3
		CI9274		J-762-1		Y877--4-2
		Clintford		J706-1		Y877-7-2
		D669-5-3		J740		Y877-8-4
		D694-1-8		L986-1		Y907-7-2
		D698-3-1		N-289-9		Y908-4-3
		D699-4-3		N111-5		Y908-4-5
		D699-8-6		N314-3		Y908-4-8
		D700-1-6		N337-4		Y930-3-6
		D947-9-8		N364-2		Y930-4-6
		High oil #3		X2-1	2	Y930-6-5
		High oil #7		Y33-2-8		Y947-2-5

Appendix 2

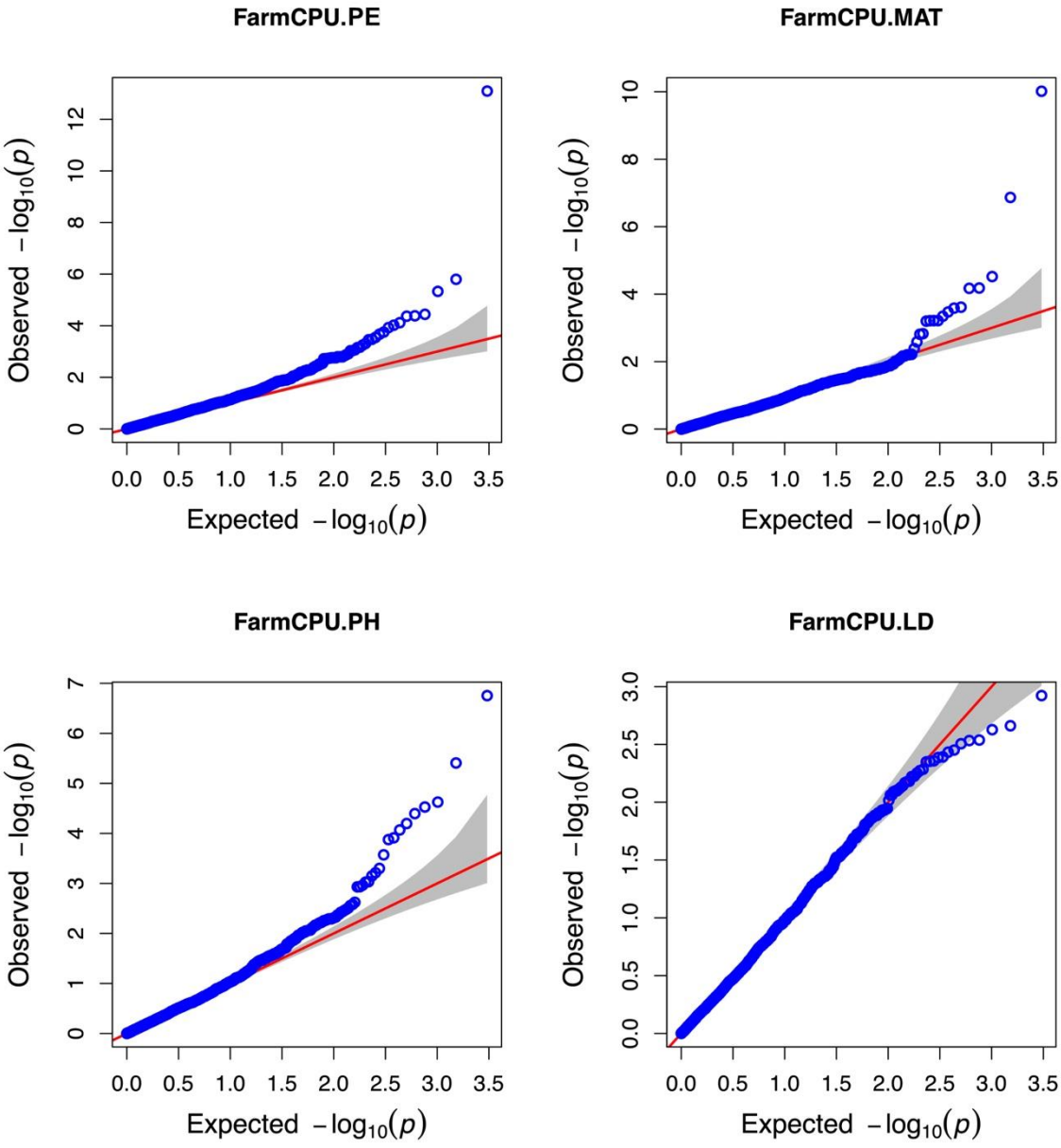
Comparison of the normalized scoring indexes and assessment methods used for maturity and lodging evaluations in Iceland and Norway.

Maturity		
Normalized index score	Iceland, index score	Norway, days from sowing to maturity
1	1	108
5.7		107
10.4		106
13.4	2	
15.1		105
19.9		104
25.8	3	
24.6		103
29.3		102
38.1	4	101
38.7		100
43.4		99
50.5	5	
48.1		98
52.9		97
54.3		
57.6		96
62.3		95
62.9	6	
67		94
71.7		93
75.3	7	
76.4		92
87.6	8	
81.1		91
85.9		90
90.6		89
95.3		88
100	9	87

Lodging		
Normalized index score	Iceland, index score	Norway, percentage of plot affected by lodging
0	1	0 %
10		10 %
12.5	2	
20		20 %
25	3	
30		25 %
37.5	4	
40		40 %
50	5	50 %
60		
62.5	6	
70		70 %
75	7	
80		70 %
87.5	8	
90		90 %
100	9	100 %

Appendix 3

Quantile-quantile (Q-Q) plots of the GWAS data using the FarmCPU model with the six principal components covariates. Abbreviations refer to: days to panicle emergence (PE), maturity score (MAT), plant height (PH), lodging score (LD).



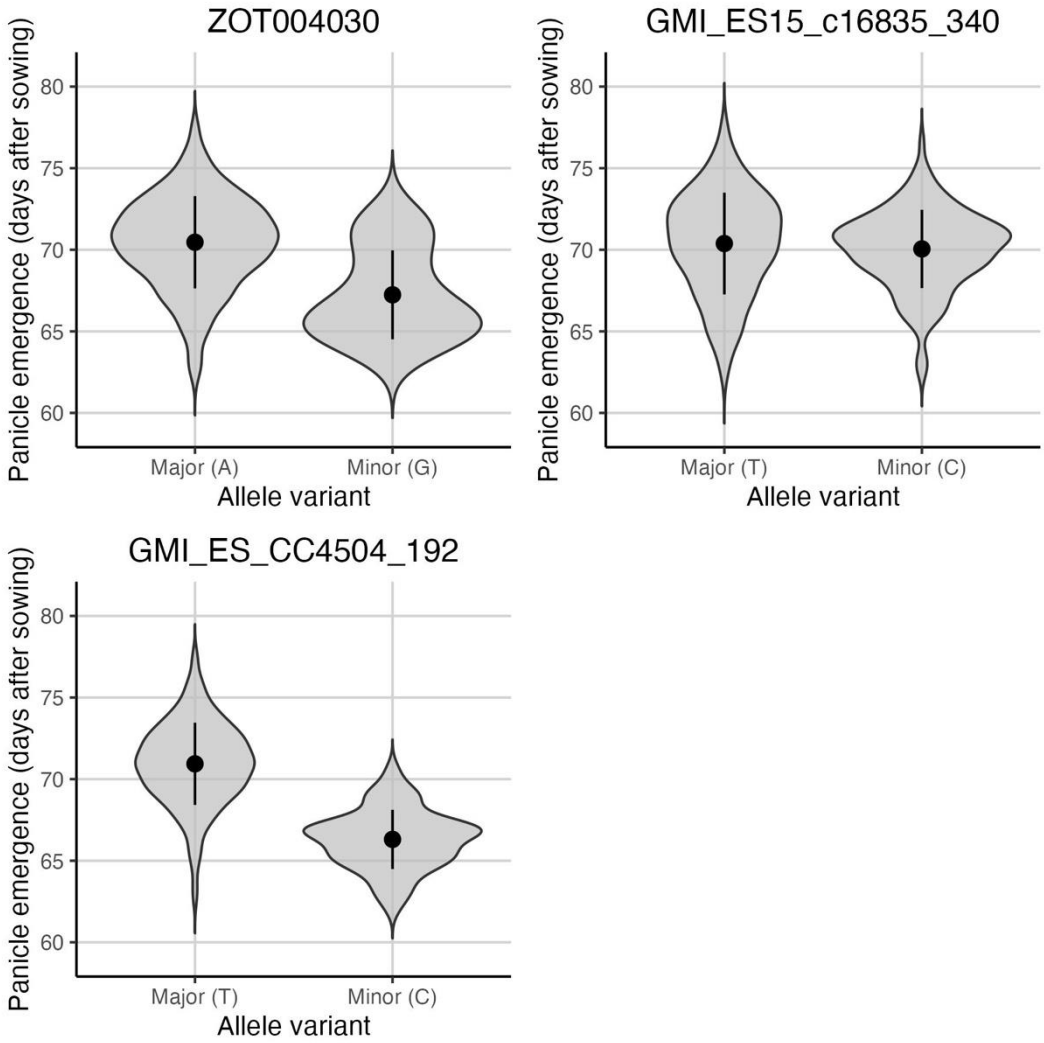
Appendix 4

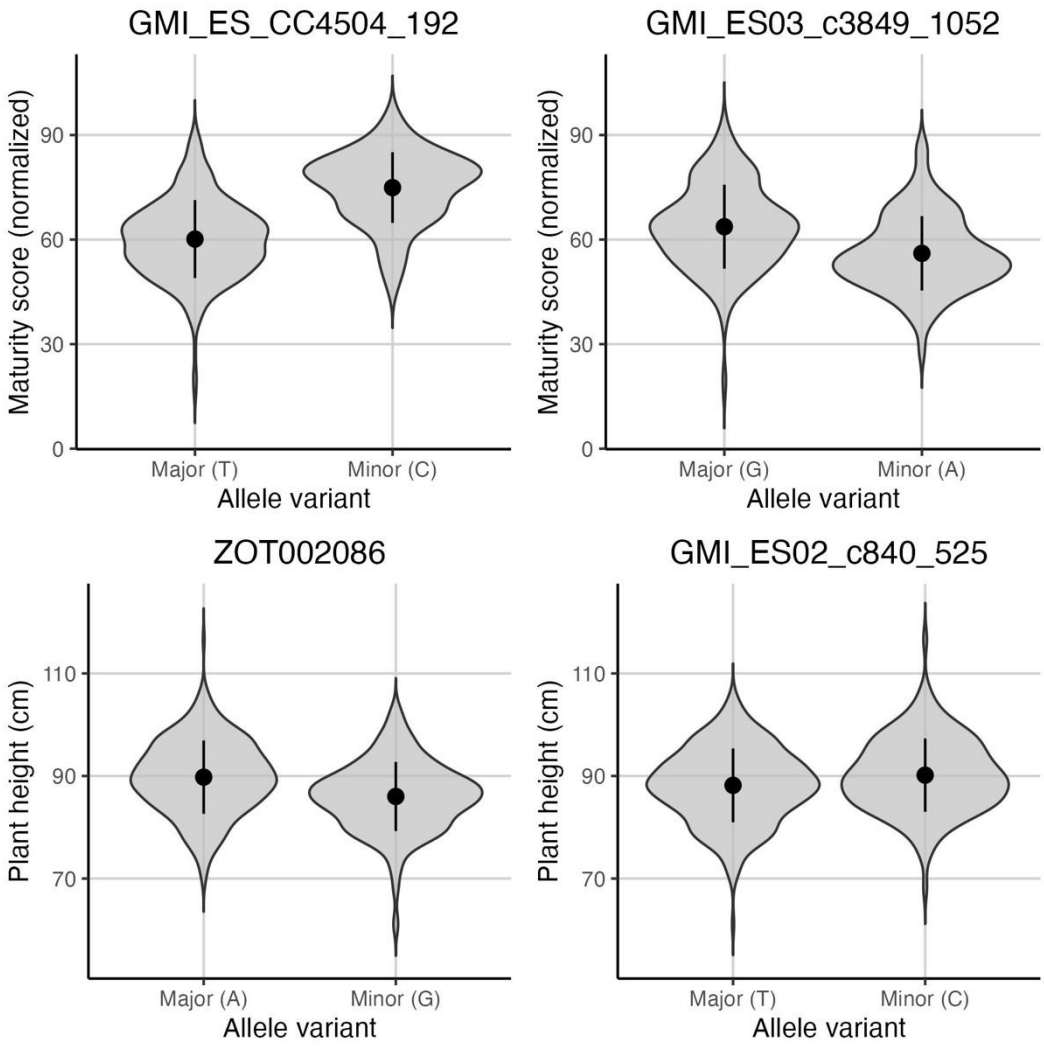
Variance, standard deviation (Std Dev), and genetic correlation for panicle emergence (PE), maturity, plant height, and lodging, estimated across locations, derived from Model *d*.

Trait	Variable	Variance	Std Dev	Correlation
PE	Iceland	14.06	3.75	
	Norway	4.81	2.19	0.84
	Residual	1.67	1.29	
Maturity	Iceland	249.03	15.781	
	Norway	29.29	5.412	1
	Residual	135.58	11.644	
Plant height	Iceland	89.72	9.472	
	Norway	18.05	4.249	0.76
	Residual	85.5	9.247	
Lodging	Iceland	125.4	11.2	
	Norway	505.4	22.48	0.3
	Residual	403.8	20.1	

Appendix 5

Violin plots visualising relationships between mean value of traits and allele variant present at loci of the marker of the significant marker-trait association.




GMI_ES_CC4504_192
Maturity score (normalized)
90
60
30
0
Major (T)
Minor (C)
Allele variant
GMI_ES03_c3849_1052
Maturity score (normalized)
90
60
30
0
Major (G)
Minor (A)
Allele variant
ZOT002086
Plant height (cm)
110
90
70
Major (A)
Minor (G)
Allele variant
GMI_ES02_c840_525
Plant height (cm)
110
90
70
Major (T)
Minor (C)
Allele variant

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