

## ORIGINAL RESEARCH ARTICLE

## Crop Breeding &amp; Genetics

# Historical grain yield genetic gains in Norwegian spring wheat under contrasting fertilization regimes

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## Abstract

Spring wheat is currently dominating wheat production in Norway. The introduction of combine harvesting in the 1950s spurred breeding efforts to improve lodging and preharvest sprouting resistance, and to integrate good breadmaking quality in the locally adapted germplasm. Release of landmark cultivars Runar and Reno in the 1970s revitalized the country's production and marked the onset of modern wheat cultivation in Norway. Since that time, new cultivars have been developed but little is known about the genetic basis of the achieved yield gains. We collected 21 representative cultivars released since 1972 in Norway and tested them in a multiyear field trial including two fertilization rates: 75 and 150 kg ha<sup>-1</sup> N. We assessed grain yield, plant height, heading, maturity, length of grain filling period, grain protein content, protein yield, aboveground biomass, harvest index, grain weight, test weight, grains per spike, grains per square meter, and spikes per square meter and their response to fertilization. We document an annual increase in grain yield of 17.8 kg ha<sup>-1</sup> (0.34%), at both rates of N fertilization. None of the traits exhibited significant genotype × management interaction. Wheat breeding has led to the development of higher-yielding cultivars with higher protein yield that mature later, have a prolonged grain-filling period, and produce more grains per spike and grains per unit area.

## 1 | INTRODUCTION

Wheat cropping in Norway is challenged by several factors. Severe winters limit winter wheat production and a short vegetation period causes moderate yields (on average 4.5 Mg ha<sup>-1</sup>, data from 2003 to 2019; Statistics Norway, 2020), as compared with averages of other European countries with more productive systems (France, 6.98 Mg ha<sup>-1</sup>; Germany, 7.52 Mg ha<sup>-1</sup>; Ireland, 9.12 Mg ha<sup>-1</sup>; and the United King-

dom, 7.92 Mg ha<sup>-1</sup>) (FAOSTAT, data from 2003 to 2019; <https://www.fao.org/faostat/en/#home>). Additionally, the wet and windy climate, especially during late season, caused delayed harvest in many years and further promotes production challenges such as preharvest sprouting, lodging, and diseases like powdery mildew, fusarium head blight, and septoria nodorum blotch (Lillemo & Dieseth, 2011).

To deal with those limitations, experimental work in agriculture was initiated in Norway in 1889, quickly being followed by introducing artificial fertilizers and new cultivars. During the 1889–1962 period, wheat yields increased by approximately 13 kg ha<sup>-1</sup> per year, of which 52.6% were estimated to come from introduction of new cultivars and 47.4%

**Abbreviations:** BM, biomass; DM, days to maturity; GF, grain filling period; GPC, grain protein content; GrPm2, grains per m<sup>2</sup>; GY, grain yield; HI, harvest index; PC, principal component; PH, plant height; PY, protein yield; TKW, thousand-kernel weight; TW, test weight.

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from improved growing technique (Strand, 1964). From 1960 to 1974, spring wheat yields were increased further by approximately 130 kg ha<sup>-1</sup> per year (Strand, 1975), and the 1960–1992 period yielded, in total, an annual increase of 74 kg ha<sup>-1</sup> per year, with 47% attributed to new cultivars, 22% to management, and 31% to a combination of new cultivars and management (Strand, 1994). However, little is known about recent yield progress in Norwegian spring wheat cropping.

Cultivars grown in Norway before the 1950s were susceptible to lodging, and thus had to be either windrowed or manually harvested and dried indoors due to the weather conditions in the late growing season. This rendered them not eligible to fully benefit from mechanization (single-pass harvesting) and increased use of N fertilization. The lack of fit between available cultivars and the new agronomic practice coupled with low import prices resulted in little stimulation of domestic production, nearly eradicating spring wheat in the 1960s. This spurred breeding efforts that eventually resulted in the release of two landmark cultivars, Runar and Reno (introduced in 1972 and 1975, respectively), which showed enough resilience to the Norwegian growing conditions to revitalize the wheat cropping and mark the beginning of the era of modern wheat cultivation in Norway (Lillemo & Dieseth, 2011).

Research on yield genetic gains in many wheat collections revealed that it is associated with an increase in the number of kernels per spike and kernels per unit area whereas the kernel weight has remained constant or decreased (Flohr et al., 2018; Lo Valvo et al., 2018; Sayre et al., 1997; Voss-Fels et al., 2019). The increase in kernels per spike is mostly due to the introduction of the Norin 10 dwarfing alleles *Rht-B1b* and *Rht-D1b* (Foulkes et al., 2007), which have been spread around the world with the CIMMYT germplasm used in breeding programs (Mjærnum, 1992). Shortening of the straw had little effect on spike architecture; the number of spikelets per spike is unaffected, but the above-mentioned dwarfing genes are known to increase spike fertility because less assimilates are needed for the growth and elongation of stems in semi-dwarf wheat cultivars (Fischer & Stockman, 1986; Miralles et al., 1998). Yield gains are contingent on increasing biomass produced while maintaining or improving harvest index (HI) in winter wheat (Beche et al., 2014). The effects of dwarfing genes on yield and HI are mostly explained by the reduced competition for assimilates between the straw and the spike during stem elongation, resulting in an increased sink size, yielding an increased seed number (Uddin & Marshall, 1989). Yield genetic gain drivers from various collections often overlap, but it is still necessary to investigate each set because each set has distinct characteristics and pedigrees. This knowledge is essential to maintain breeding progress by evaluating gains achieved and pointing out traits that can be emphasized in future breeding (Reynolds et al., 2009; Wu et al., 2014).

### Core Ideas

- Grain yield in the 1972–2019 period increased by 17.8 kg ha<sup>-1</sup> (0.34%) per year due to improved cultivars.
- Grain yield gains do not rely on intensive N fertilization.
- Cultivars do not exhibit significant genotype × management interactions for any of the measured traits.
- Breeding in Norway since 1972 caused the cultivars to have a 2-d longer grain-filling period and reach physiological maturity 3 d later.
- New cultivars in Norway produce more grains per spike and grains per unit area.

Historically, yield gains have been attributed to genetic progress and crop management in equal measure. However, it is not uncommon to observe a significant contribution of the interaction between genotype and management to the yield progress (Strand, 1964). The annual genetic yield gain in high-intensity wheat systems since the 1960s has been approximately 1% per year (Abbate et al., 1998; Sayre et al., 1997; Shearman et al., 2005). However, there is an ongoing discussion as to whether the genetic gains continue or whether they are approaching a plateau phase (Grassini et al., 2013).

It has been shown that the development of new cultivars usually leads to improvement in yield, regardless of agronomic practice. The performance is consistently better under both high and low inputs (Ahlemeyer & Friedt, 2011; Ahrends et al., 2018; Voss-Fels et al., 2019). This defies the view that genetic gains are observed only under intense management and proves that novel cultivars are better adapted to their target environments.

The objectives of this study were: (a) to estimate and document grain yield (GY) progress in Norwegian spring wheat over the course of the last five decades, (b) to determine if this progress relies on N fertilization input, (c) to determine the yield components linked to this increase, and (d) to determine and document wheat agronomical trait changes over this period.

To achieve these goals, we performed a multiyear study of historical and current spring wheat cultivars present on the Norwegian market between 1972 and 2019. We assessed genetic gains in GY, yield-related and physiological traits over the course of five decades, their response to agronomical input, and the underlying traits associated with the GY increase.

**TABLE 1** Overview of the cultivars used in the study, countries of origin, breeders, and years of release

Line	Cultivar	Country/breeder	YOR <sup>a</sup>
1	Runar	Norway/IPK	1972
2	Reno	Norway/IPK	1975
3	Tjalve	Sweden/Weibull	1987
4	Bastian	Norway/IPK	1989
5	Polkka	Sweden/Lantmännen SW Seed	1992
6	Avle	Sweden/Lantmännen SW Seed	1996
7	Zebra	Sweden/Lantmännen SW Seed	2001
8	Bjarne	Norway/Graminor	2002
9	Demonstrant	Norway/Graminor	2008
10	Krabat	Norway/Graminor	2010
11	Mirakel	Norway/Graminor	2012
12	Rabagast	Norway/Graminor	2013
13	Seniorita	Norway/Graminor	2014
14	Arabella	Poland/Danko	2014
15	Willy	Norway/Graminor	2016
16	Caress	Sweden/Lantmännen SW Seed	2017
17	Zombi	Norway/Graminor	2018
18	Alarm	Norway/Graminor	2019
19	Betong	Norway/Graminor	2019
20	Eleven	Sweden/Lantmännen SW Seed	2019
21	Felgen	Sweden/Lantmännen SW Seed	2019

<sup>a</sup>YOR, year of release. The year when a cultivar was listed in Norway after passing official trials.

## 2 | MATERIALS AND METHODS

### 2.1 | Plant material

We assembled a collection of 21 spring wheat cultivars released in Norway, covering historically the most widely cultivated material since 1972 as well as the current and recently released cultivars (Table 1). It represents the breeding progress achieved from 1972 (onset of modern wheat cultivation in Norway) to the present day. Except for the cultivar “Arabella,” which is of Polish origin, all the other cultivars were developed in either Norway or Sweden. The year when a cultivar was officially approved by the Plant Variety Board (year of release) was used to place it on the timeline. At the start of the field experiment in 2016, cultivars 16–21 (Table 1) were still undergoing official trials and were released in the following years. Additionally, our trials included three breeding lines that were either withdrawn or rejected from official trials during the period. Those lines remained in our field trials but data from those was excluded from the analysis after lsmeans calculation.

The collection was assembled to maximize its relevance for the actual market situation over the period; therefore, the col-

lection suffers from imbalance as the cultivars are not equally distributed on the timeline. Cultivars Runar and Reno had almost 100% market share until the release of Tjalve in 1987, which creates a 12-yr gap between 1975 and 1987. We did not attempt to forcibly fill this gap as it would decrease the collections' relevance. Recent years were marked with the release of more cultivars to the market; therefore, the 2008–2019 period includes a relatively large number of accessions (Table 1).

### 2.2 | Field trials

We conducted the experiment in field seasons 2016–2020 at Vollebakk Research Station (Ås, southeastern Norway, 59°39' N, 10°45' E). This location represents the most important southern wheat cropping region in Norway. Field season 2018 was excluded from the analysis presented in the main text due to drought (Supplemental Figure S1; Table 2) but is presented separately in the Supplemental Material. To evaluate the effect of fertilization rates on yield performance and physiological traits, two rates (managements) were applied before sowing: 75 and 150 kg ha<sup>-1</sup> N (referred to as lowN and highN, respectively) of compound NPK fertilizer (YaraMila 22–3–10). The highN treatment reflects typical fertilization rates for spring wheat in Norway currently, whereas the lowN treatment was included to assess the performance of the cultivars under less intensive management. Field trials included the full set of 24 cultivars and were arranged in randomized incomplete block split-plot design with two replicates per management and block size of six, with the position of the main treatment (fertilization level) and subtreatments (cultivar) being randomized every year. Trial plots of 5 m by 1.5 m arranged in eight rows with 30-cm spacing between neighboring plots were seeded with 185 g of kernels (61, 7 g m<sup>-2</sup>); 1-m alleys were sprayed out with glyphosate after emergence, leaving plots of 4-m length for harvest. Trials were sown on 12 May 2016, 24 May 2017, 3 May 2019, and 20 Apr. 2020. Following the seeding, standard local agronomic practice was followed to keep the trial plots free of weeds and plant diseases by use of herbicides (Tripali [active ingredients: florasulam + metsulfuron-methyl + tribenuron-methyl] and/or Duplosan Meko [mekoprop]), and fungicides (Proline [prothioconazole], Aviator Xpro [bixafen + prothioconazole], Forbel [fenpropimorph], and/or Comet Pro [pyraclostrobin]) at recommended doses according to needs. Border rows were planted with buffer cultivar (Bastian) to eliminate border effects. Following ripening, samples were gathered for yield component estimation and the remaining trial material was combine harvested during the first 2 wk of September.

Weather conditions throughout the field trial years were similar in terms of average monthly temperature, solar radiation, and rainfall except for the 2018 season (Table 2).

TABLE 2 Weather data for the field trial seasons 2016–2020 between April and September

Month	2016			2017			2018			2019			2020		
	T <sub>avg</sub>	Rf <sub>sum</sub>	Ir <sub>avg</sub>	T <sub>avg</sub>	Rf <sub>sum</sub>	Ir <sub>avg</sub>	T <sub>avg</sub>	Rf <sub>sum</sub>	Ir <sub>avg</sub>	T <sub>avg</sub>	Rf <sub>sum</sub>	Ir <sub>avg</sub>	T <sub>avg</sub>	Rf <sub>sum</sub>	Ir <sub>avg</sub>
	°C	mm	W m <sup>-2</sup>	°C	mm	W m <sup>-2</sup>	°C	mm	W m <sup>-2</sup>	°C	mm	W m <sup>-2</sup>	°C	mm	W m <sup>-2</sup>
Apr.	5.2	100	11.7	4.4	35	13.4	5.1	32	14.0	7.9	15	16.2	6.4	30	15.0
May	11.6	50	18.5	9.6	68	14.6	15.0	0	22.2	9.7	101	17.0	9.5	47	21.4
June	15.6	90	21.1	14.3	94	19.1	16.7	82	23.9	14.8	64	17.7	17.6	115	21.1
July	16.1	55	19.1	15.9	20	19.8	20.2	44	23.2	17.2	52	20.2	14.3	128	18.0
Aug.	14.6	140	14.1	14.5	104	14.9	15.4	21	14.2	16.2	110	13.7	16.2	51	15.7
Sept.	14.1	41	9.9	11.5	119	6.7	12.1	128	9.4	11.0	191	8.3	12.0	81	9.0

Note. Ir<sub>avg</sub>, average solar radiation; Rf<sub>sum</sub>, sum of monthly rainfall; T<sub>avg</sub>, average temperature.

TABLE 3 Overview of the gathered traits, abbreviations, units, and seasons when the data was collected

Trait	Abbreviation	Unit	Collected
Grain yield	GY	Mg ha <sup>-1</sup>	2016, 2017, 2019, 2020
Plant height	PH	cm	2016, 2017, 2019, 2020
Days to heading	DH	day	2017, 2019, 2020
Days to maturity	DM	day	2016, 2017, 2019, 2020
Grain filling period	GF	day	2017, 2019, 2020
Thousand-kernel weight	TKW	g	2016, 2017, 2019, 2020
Test weight	TW	g	2016, 2017, 2019, 2020
Grain protein content	GPC	%	2016, 2017, 2019, 2020
Protein yield	PY	g m <sup>-2</sup>	2016, 2017, 2019, 2020
Biomass	BM	g 50 stems <sup>-1</sup>	2019, 2020
Harvest index	HI	ratio	2019, 2020
Grains per spike	GrPS	spike <sup>-1</sup>	2017, 2019, 2020
Grains per area	GrPm2	grains m <sup>-2</sup>	2016, 2017, 2019, 2020
Spikes per area	SpPm2	spikes m <sup>-2</sup>	2017, 2019, 2020

Season 2018 was marked with higher average temperatures, no rainfall, and high solar radiation from the second half of April until early June, which, despite irrigation efforts, caused severe drought stress to the trial and shortened the growing season by nearly a month. Data from season 2018 was unrepresentative compared with the “normal” growing seasons, and therefore, was analyzed separately.

Daily weather data were downloaded from the Norwegian Bioeconomy Institute weather service, station in Ås (<https://lmt.nibio.no/station/5/>).

### 2.3 | Measurements

Cultivars were evaluated for GY, plant height (PH), heading and physiological maturity, yield components (test weight [TW], thousand-kernel weight [TKW], and grains per spike), grain protein content (GPC), and aboveground biomass (BM) at maturity. Based on these variables, additional parameters such as protein yield (PY), HI, grains per area, and spikes per

area were derived. Not every trait was assessed in every season (Table 3).

Assessment of heading and maturity stages was performed visually, recording the date when 50% of the plants were in the respective stage.

Plant height was measured manually at crop maturity as an average height of a sample of fertile stems, from soil bed to the top of a spike (excluding awns, if they were present).

Aboveground biomass was estimated by weighing 50 randomly selected, moisture equalized (dried at 30 °C for 5 d) fertile mature tillers. Those samples were manually threshed to estimate grains per spike.

Protein content was determined by near infrared reflectance spectroscopy on full kernels using Perten Inframatic 9200 spectrometer (Perten Instruments AB).

Grain yield per plot was dried to 13.5% moisture content, weighed, and converted to Mg ha<sup>-1</sup>. A subsample of kernels was used to estimate TKW and TW.

Protein yield was calculated as GY multiplied by protein content, number of grains per m<sup>2</sup> (GrPm2) as GY divided

by TKW, and number of spikes per m<sup>2</sup> as number of GrPm2 divided by grains per spike. Harvest index was calculated as a ratio between the grain weight per 50 spikes and the biomass of 50 fertile tillers. Collecting only fertile tillers for HI estimation causes high HI values as the proportion of infertile stems is not considered.

## 2.4 | Data analysis

All calculations and analyses were performed in R version 4.05. Least square estimates for traits across trial years and designs were calculated using packages “lme4” and “lmerTEST” according to the following mixed model:

$$P_{ijklnos} = \mu + g_i + m_j + g \times m_{ij} + Y_k + Y : R_{kl} + Y : R : B_{kln} + Y : W_{ko} + Y : C_{ks} + e_{ijklnos}$$

where  $P_{ijklnos}$  is the phenotype (trait value) of the  $i$ th cultivar in the  $j$ th management (fertilization) grown in the  $k$ th field year in the  $l$ th replicate in the  $n$ th block in the  $o$ th row and  $s$ th column;  $\mu$  is the general mean,  $g_i$  is the fixed effect of the  $i$ th cultivar,  $m_j$  is the fixed effect of the  $j$ th management,  $g \times m_{ij}$  is the fixed effect of the  $i$ th cultivar grown under  $j$ th management (interaction),  $Y_k$  is the random effect of  $k$ th field year,  $Y : R_{kl}$  is the random effect of the  $l$ th replicate within  $k$ th field year,  $Y : R : B_{kln}$  is the random effect of the  $n$ th block within the  $l$ th replicate within  $k$ th field year,  $Y : W_{ko}$  is the random effect of the  $o$ th field row within the  $k$ th field year,  $Y : C_{ks}$  is the random effect of the  $s$ th field column within the  $k$ th field year, and  $e_{ijklnos}$  represents the error term. Fixed effects are denoted as lowercase letters, random effects are denoted by uppercase letters, interaction is indicated by “ $\times$ ”, and nesting is indicated by “:”. Row and column random effects (denoted  $W$  and  $C$  in the model, respectively) were added to additionally correct for variability within the field on top of the block effects if a spatial trend was apparent. Model 1 was used to calculate lsmeans averaged over genotypes or managements and to perform ANOVA based on the estimated fixed effects. Degrees of freedom were calculated according to Satterthwaite’s method.

The lsmeans were calculated based on the full experiment with 24 cultivars (including the three lines that were rejected) to take full advantage of the trial design. The three rejected lines were removed from the analysis after lsmeans calculation.

For the estimation of trait changes over the 1972–2019 period, a linear model was used with lsmeans of trait value as a response variable and year of release as an independent variable. Other models were investigated (quadratic, cubic, and polynomial), but those more complex curves did not explain significantly more variance and were potentially overfit as our sample of cultivars is small and imbalanced. Therefore,

we decided to use standard linear regression for the purpose of documenting and estimating the changes in traits over the period.

For the traits that showed improvement over the period (correlation with year of release  $>0.3$ ), genetic gains per year were reported as absolute values and as percent of the predicted trait value for year 1972 (earliest cultivar in the collection) to standardize the results. Traits that showed improvement under at least one treatment level were displayed in Figure 4.

Principal component analysis was performed on least squares trait estimates for either cultivars alone or cultivars in particular management. To account for the effect of scale, variables were scaled as 1/SD.

Results were visualized using R packages: “corrplot,” “ggplot2,” “ggpubr,” and “ggmisc.”

## 3 | RESULTS

### 3.1 | Grain yield

Weather conditions throughout the field trial years were similar in terms of temperature and rainfall, except for the 2018 season (Supplemental Figure S1) when heat and drought stress reduced yields by nearly 70%, which can be seen in the average GY of 6.01, 5.81, 5.70, and 5.35 Mg ha<sup>-1</sup> in seasons 2016, 2017, 2019, and 2020, respectively, compared with 1.91 Mg ha<sup>-1</sup> in 2018 (Supplemental Table S1). Achieved GYs in the representative seasons are significantly higher than the national long-term average of approximately 4.5 Mg ha<sup>-1</sup>. The highest-yielding cultivar in the collection is Arabella (released in 2014, 6.5 Mg ha<sup>-1</sup>) and the lowest-yielding is Runar (released in 1972, 5.2 Mg ha<sup>-1</sup>). Significant ( $p < .05$ ) annual genetic gains in GY over the 1972–2019 period are observed for all the trial years and their mean except for field season 2017 (Table 4; Supplemental Table S1). Estimated annual genetic gain in GY vary from 16 kg ha<sup>-1</sup> (0.33%, Season 2020) to 23.1 kg ha<sup>-1</sup> (0.47%, Season 2019; Supplemental Table S1), averaging 17.8 kg ha<sup>-1</sup> (0.34%) per year (Table 4). Correlation between GY and year of release of a cultivar is subject to variation among the years (ranging from 0.64 to 0.73) whereas being the strongest for the average values (0.74) (Table 3; Supplemental Table S1). Genetic gains in GY can also be observed under severe drought stress; on average 6 kg ha<sup>-1</sup> (0.39%) per year, 10.3 kg ha<sup>-1</sup> (0.60%) under highN, and 2.8 kg ha<sup>-1</sup> (0.17%) under lowN (Supplemental Table S1).

Grain yield is significantly ( $p < .001$ ) affected by fertilization level and cultivar. Estimated GY averaged over trial seasons for the 75 kg ha<sup>-1</sup> (lowN) and 150 kg ha<sup>-1</sup> (highN) fertilization levels are 4.99 and 6.52 t ha<sup>-1</sup>, respectively. No significant ( $\alpha = .05$ ) interaction among genotypes and fertilization levels is observed (Figure 1; Table 5) for GY. Genetic gains over the period are observed for both fertilization

TABLE 4 Trait estimates for cultivars in the trial averaged over fertilization levels, their mean, correlation with year of release of a cultivar, and achieved genetic gains per year

Cultivar	YOR	GY	PH	DH	DM	GF	TKW	TW	GPC	PY	BM	HI ratio	GrPS	GrPm2	SpPm2
		Mg ha <sup>-1</sup>	cm	cm	day		g	g	%	g m <sup>2</sup>	g		10 <sup>3</sup> m <sup>-2</sup>	10 <sup>3</sup> m <sup>-2</sup>	m <sup>-2</sup>
Runar	1972	5.18	90.4	55.1	105.8	50.7	39.2	79.0	11.46	59.34	93.4	0.448	25.96	13.19	508.25
Reno	1975	5.19	95.3	55.8	106.9	51.1	38.3	78.8	11.30	58.66	104.9	0.429	29.44	13.54	460.05
Tjalve	1987	5.53	79.5	58.1	107.2	49.1	37.3	77.2	11.58	64.03	85.0	0.467	28.59	14.82	518.27
Bastian	1989	5.32	74.3	54.6	105.4	50.8	34.2	78.0	12.07	64.23	82.4	0.440	25.27	15.54	614.88
Polkka	1992	5.26	89.1	57.5	105.7	48.2	35.8	78.2	11.75	61.75	85.2	0.430	28.23	14.69	520.17
Avle	1996	5.51	79.8	57.4	107.8	50.4	34.5	76.5	12.08	66.53	86.0	0.472	29.32	15.95	544.11
Zebra	2001	5.68	87.5	56.2	109.4	53.3	40.0	78.2	11.46	65.14	94.4	0.436	28.67	14.19	495.02
Bjarne	2002	5.86	72.4	56.4	106.5	50.1	37.0	77.1	11.28	66.15	80.2	0.489	26.84	15.84	590.03
Demonstrant	2008	6.09	80.1	57.9	109.5	51.6	39.8	79.6	10.51	63.97	96.3	0.471	29.21	15.30	523.72
Krabat	2010	5.71	77.0	58.4	108.1	49.7	37.2	77.9	11.20	63.92	89.4	0.463	30.85	15.35	497.55
Mirakel	2012	5.82	91.0	57.6	107.2	49.6	37.7	77.6	11.16	64.72	91.0	0.439	28.46	15.43	542.18
Rabagast	2013	5.44	71.7	58.0	107.5	49.5	34.3	78.0	11.32	61.53	72.3	0.440	25.69	15.84	616.30
Seniorita	2014	5.66	85.5	58.7	109.3	50.5	35.3	79.4	11.58	65.55	87.6	0.433	29.27	16.04	547.91
Arabella	2014	6.50	82.6	55.1	110.2	55.0	39.8	77.5	10.70	69.51	95.7	0.485	30.75	16.34	531.24
Willy	2016	5.79	80.1	56.7	109.6	52.9	36.0	76.5	10.55	61.09	93.9	0.466	30.78	16.09	522.54
Caress	2017	5.69	76.8	57.1	108.7	51.7	37.3	78.3	10.75	61.15	87.1	0.475	29.27	15.25	521.00
Zombi	2018	5.80	75.2	56.2	106.8	50.5	38.0	80.9	12.17	70.52	90.8	0.470	29.02	15.24	525.30
Alarm	2019	5.88	82.8	56.8	109.6	52.9	34.6	78.2	11.29	66.31	91.9	0.443	30.07	16.96	564.17
Betong	2019	6.08	82.0	56.3	109.2	52.9	39.4	77.9	11.19	68.05	93.2	0.446	27.55	15.43	559.94
Eleven	2019	6.08	83.1	55.6	109.7	54.1	43.8	79.3	10.55	64.19	103.0	0.471	28.03	13.89	495.66
Felgen	2019	6.20	82.1	57.1	109.7	52.6	37.2	79.8	10.75	66.71	99.5	0.469	32.85	16.66	507.08
mean ± SD		5.73 ± 0.34	81.8 ± 6.02	56.8 ± 1.15	108.1 ± 1.53	51.3 ± 1.76	37.5 ± 2.38	78.3 ± 1.17	11.27 ± 0.49	64.43 ± 3.09	90.6 ± 7.4	0.456 ± 0.018	28.77 ± 1.79	15.31 ± 0.98	533.59 ± 39.05
r <sup>a</sup>		0.74***	0.40 <sup>†</sup>	0.27 <sup>†</sup>	0.70***	0.43*	0.08 <sup>†</sup>	0.15 <sup>†</sup>	-0.44*	0.55*	0.033 <sup>†</sup>	0.31 <sup>†</sup>	0.42 <sup>†</sup>	0.64**	0.19 <sup>†</sup>
Genetic gain <sup>b</sup>		0.0178-0.34%	-0.17-0.19%	-	0.072 ± 0.07%	0.051-0.1%	-	-	-0.015-0.13%	0.11-0.19%	-	0.0004-0.09%	0.052-0.19%	0.04-0.30%	-

Notes. BM, biomass; DH, days until heading; DM, days until maturity; GF, length of grain filling period; GPC, grain protein content; GrPm2, grains per square meter; GrPS, grains per spike; GY, grain yield; HI, harvest index; PH, plant height; PY, protein yield; SpPm2, spikes per square meter; TKW, thousand-kernel weight; TW, test weight; YOR, year of release.

<sup>a</sup>Correlation with year of release of a cultivar.

<sup>b</sup>Per annum, expressed as an absolute value and as % of the predicted value for year 1972.

\*Significant at the .05 probability level. \*\*Significant at the .01 probability level. \*\*\*Significant at the .001 probability level. †N.S, nonsignificant.

**TABLE 5** Traits collected in the study, units, abbreviations, least squares estimates of an average of trait values within management levels and significance of model parameters genotype (g), management (fertilization, m) and genotype × management (g × m)

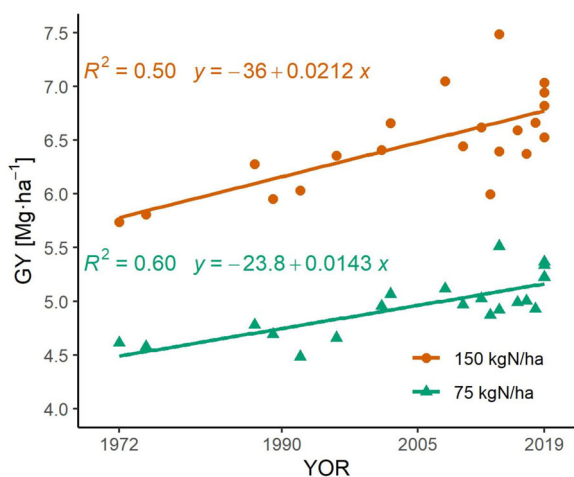
Trait	Unit	Estimate ± SE <sup>a</sup>		Significance of model parameters <sup>b</sup>		
				g	m	g × m
		75 kg ha <sup>-1</sup> N	150 kg ha <sup>-1</sup> N			
GY	t ha <sup>-1</sup>	4.99 ± 0.16	6.52 ± 0.16	***	***	ns
PH	cm	80.09 ± 4.21	83.61 ± 4.21	***	***	ns
DH	day	56.95 ± 3.04	56.90 ± 3.04	***	ns	ns
GF	day	49.83 ± 3.55	52.73 ± 3.55	***	***	ns
DM	day	106.78 ± 1.45	109.63 ± 1.45	***	***	ns
TKW	g	37.29 ± 0.57	37.99 ± 0.57	***	**	ns
TW	g	78.09 ± 0.98	78.53 ± 0.98	***	***	ns
GPC	%	10.71 ± 0.32	11.76 ± 0.32	***	***	ns
PY	kg m <sup>-2</sup>	53.51 ± 2.25	76.46 ± 2.25	***	***	ns
BM	g	79.76 ± 13.07	101.72 ± 13.07	***	***	ns
HI	ratio	0.442 ± 0.02	0.473 ± 0.02	***	***	ns
GrPS	spike <sup>-1</sup>	26.52 ± 2.65	31.01 ± 2.65	***	***	ns
GrPm2	10 <sup>3</sup> m <sup>-2</sup>	13.45 ± 0.55	17.27 ± 0.55	***	***	ns
SpPm2	m <sup>-2</sup>	532.1 ± 51.8	540.5 ± 51.8	***	ns	ns

Notes. BM, biomass; DH, days until heading; DM, days until maturity; GF, length of grain filling period; GPC, grain protein content; GrPm2, grains per square meter; GrPS, grains per spike; GY, grain yield; HI, harvest index; PH, plant height; PY, protein yield; SpPm2, spikes per square meter; TKW, thousand-kernel weight; TW, test weight.

<sup>a</sup>Least squares estimate of trait value averaged over all cultivars and years.

<sup>b</sup>Two-way ANOVA.

\*Significant at the .05 probability level. \*\*Significant at the .01 probability level. \*\*\*Significant at the .001 probability level.



**FIGURE 1** Grain yield genetic gains over the 1972–2019 period under 75 kg ha<sup>-1</sup> N (green, triangles) and 150 kg ha<sup>-1</sup> N (red, dots) fertilization regimes. GY, grain yield; YOR, year of release

levels, 21.2 kg ha<sup>-1</sup> (0.37%) and 14.3 kg ha<sup>-1</sup> (0.32%) per year for highN and lowN, respectively; however, the relationship between GY and year of release is stronger under lowN ( $R^2 = .6$ ) than highN ( $R^2 = .5$ ). Cultivars released recently (2014–2019) grown under lowN nearly approach GY values of the legacy cultivars (Reno and Runar) under highN

(Figure 1). The genetic gains were positively validated in an independent multiyear field trial (Supplemental Figure S5).

### 3.2 | Agronomical and physiological traits

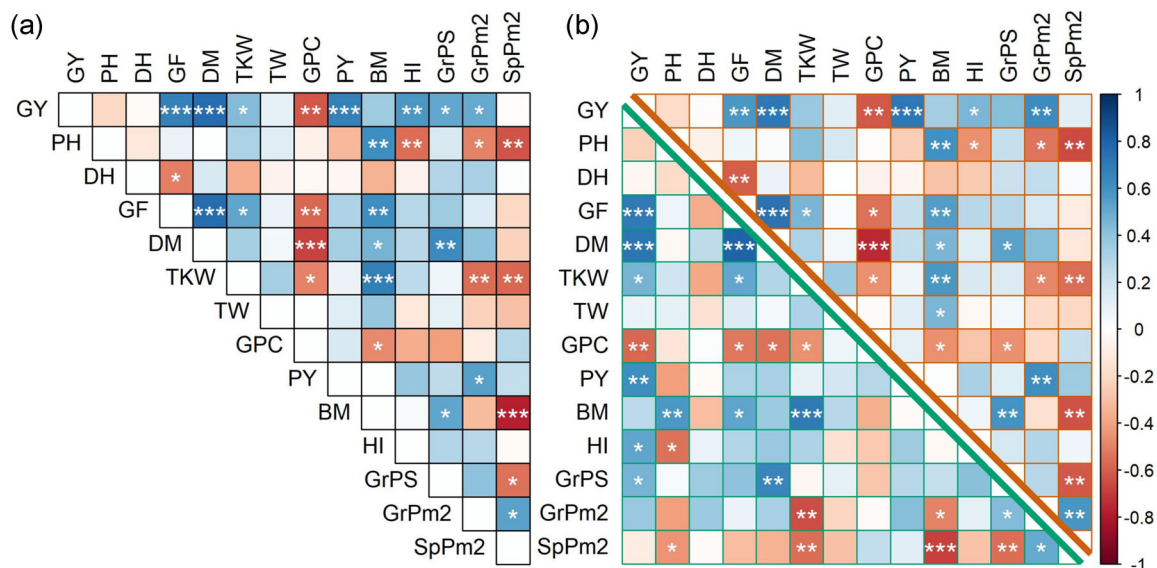
Significant genetic gains over the period were found for days to maturity (DM), length of grain filling period (GF), GPC, PY, and GrPm2 (Table 4).

None of the assessed traits were subject to genotype by management ( $g \times m$ ) interaction at 95% significance level. All traits, excluding DH and SpPm2, are strongly affected by fertilization, and significant differences among genotypes were found for every trait investigated (Table 5).

### 3.3 | Correlations among the traits

Under both managements and for their mean, GY is consistently and positively associated with GF and DM. A typical negative relationship between GPC and GY is observed; however, the relationship between GY and PY is positive and strong under both managements and their mean (Figure 2a,b).

Yield components associated with GY differ between managements: under lowN, GY is associated with TKW and



**FIGURE 2** Pearson's correlation coefficient matrices for (a) genotypic means and (b) genotypic means for traits of cultivars grown under lowN (below diagonal, green border) and highN (above diagonal, red border). BM, biomass; DH, days until heading; DM, days until maturity; GF, length of grain filling period; GPC, grain protein content; GrPm2, grains per square meter; GrPS, grains per spike; GY, grain yield; HI, harvest index; PH, plant height; PY, protein yield; SpPm2, spikes per square meter; TKW, thousand-kernel weight; TW, test weight. \*\*\* $p < .001$ , \*\* $p < .01$ , \* $p < .05$

grains per spike (GrPS); and under highN, GY correlates with the number of GrPm2. For genotypic means, differences in GY can be best explained by grains per spike increase. The length of the GF is determined by DM rather than DH. GF is associated with GY and GPC due to the negative correlation between GY and GPC. Differences in biomass produced by the cultivars can be explained to a large degree by differences in PH, which, in connection with a lack of a significant relationship between GY and PH, suggests that the decrease in PH did not reduce GY achieved by the cultivars, and therefore, improvement of HI was driven by PH reduction. Number of spikes per square meter is associated under both managements with reduced PH, TKW, and BM, hinting that cultivars producing a large number of spikes per unit area tend to be shorter, produce smaller kernels, and accumulate less biomass during growing season, and therefore, possess higher HI. Longer GF is associated with higher TKW and BM production (Figure 2a,b).

### 3.4 | Principal component analysis

The first two principal components (PCs) explain a total of 59.4% of variance present in the dataset of genotypic means of the cultivars (Figure 3a). Biplot analysis reveals a similar correlation pattern to that in Figure 3b: a strong cluster of variables (GY, DM, GF, and GrPS) contributing to the PC with the most explanatory power. The year of release of a cultivar can

be moderately explained by both PC1 ( $r = .50$ ,  $p = .021$ ) and PC2 ( $r = .62$ ,  $p = .002$ ).

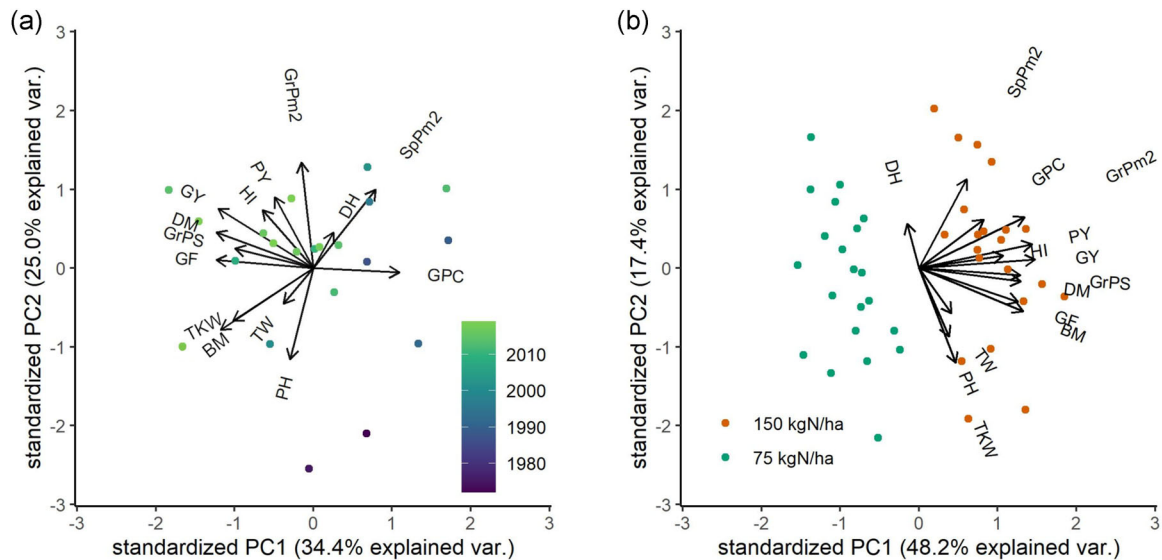
Fertilization treatment clearly clusters the genotypic means under fertilization treatments (Figure 3b). The two first PCs explain a total of 65.6% of the variance present in the dataset with mostly PC1 (capturing 48.2% of the variance) determining the management clusters. Differences among the cultivars within the same cluster are determined mostly by PC2, explaining a total of 17.4% of the variance, with TKW, TW, and PH as its biggest contributors. The traits that characterize the management clusters are mainly GrPS, DM, GY, PY, and GrPm2, confirming the findings from Table 5.

### 3.5 | Genetic gains in agronomical and physiological traits under contrasting fertilization levels

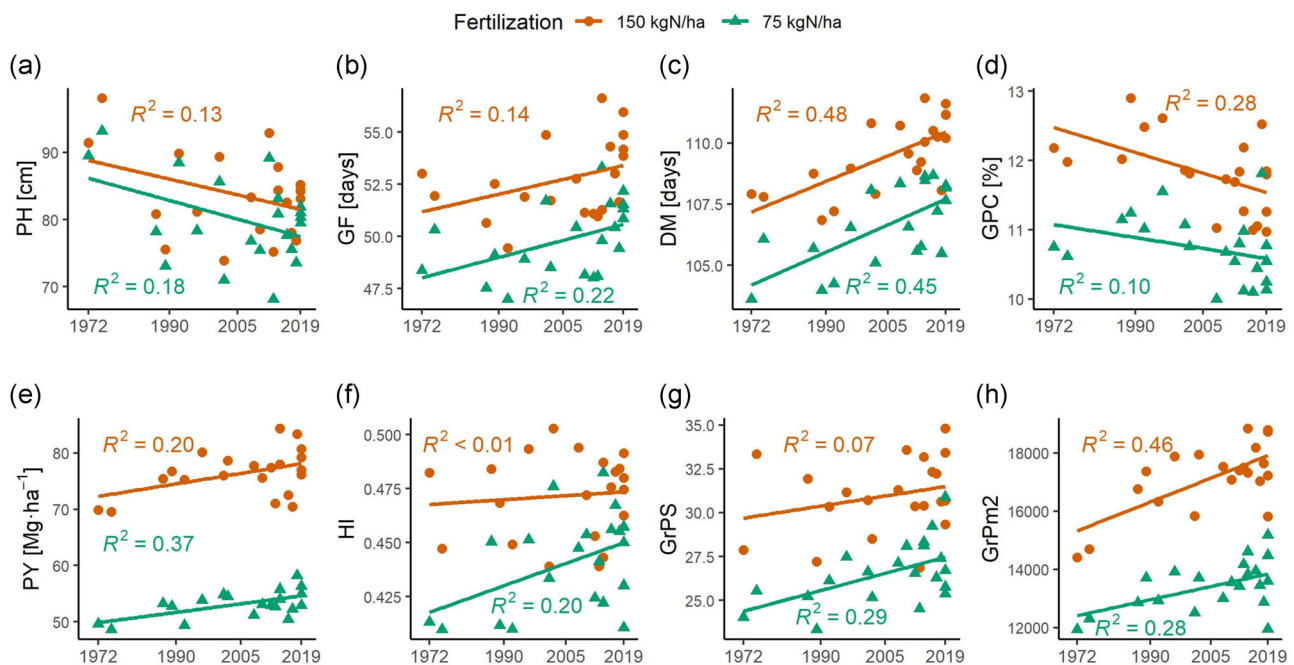
Slopes for PH, GF, DM, PY, and GrPS are not significantly different between the treatments (Figure 4a,b,c,e,g), confirming the absence of detectable  $g \times m$  interaction (Table 5). However, the slopes for GPC, HI, and GrPm2 (Figure 4d,f,h) vary between the treatments, which shows presence of minor interactions not detected by the ANOVA (Table 5).

Plant height shows a negative relationship with year of release under both treatments, but the relationship is significant only under lowN ( $\alpha = .05$ ). This association is caused by the two old cultivars (Runar and Reno, released





**FIGURE 3** Principal component (PC) analysis on (a) trait genetic estimates and (b) genetic estimates under fertilization treatments. In (a), colors are mapped to the year of release of a cultivar, in (b), colors indicate fertilization treatments. BM, biomass; DH, days until heading; DM, days until maturity; GF, length of grain filling period; GPC, grain protein content; GrPm2, grains per square meter; GrPS, grains per spike; GY, grain yield; HI, harvest index; PH, plant height; PY, protein yield; SpPm2, spikes per square meter; TKW, thousand-kernel weight; TW, test weight



**FIGURE 4** Relationships between (a) plant height, (b) grain filling period, (c) days to maturity, (d) grain protein content, (e) protein yield, (f) harvest index, (g) grains per spike, and (h) grains per m<sup>2</sup> cultivar estimates and year of release under 75 kg ha<sup>-1</sup> N (green, triangles) and 150 kg ha<sup>-1</sup> N (red, dots) fertilization. DM, days until maturity; GF, length of grain filling period; GPC, grain protein content; GrPm2, grains per square meter; GrPS, grains per spike; HI, harvest index; PH, plant height; PY, protein yield

in 1972 and 1975, respectively), showing that the newer cultivars are shorter than the old ones in Norway, but no consistent PH decrease can be documented from 1987 onward (Figure 4a).

The newer cultivars tend to have prolonged GF caused by longer DM (Figure 4b,c). Significantly ( $\alpha = .05$ ) longer GF over the period can be observed under both fertilization treatments but is stronger under lowN. The DM was

consistently increased over the period under both treatments. Cultivars released since 2018 under lowN mature in a similar time as the old cultivars (released before 1985) under highN. The length of GF and DM were increased on average by 2 and 3 d, respectively, under both treatments.

Grain protein content shows a negative correlation with year of release under both treatments, which is stronger under highN (Figure 4d). The two old cultivars (released before 1985) decrease the correlation due to their low GPC and show that GPC consistently decreased from 1985 onward. Protein yield shows a positive relation with year of release under both treatments (Figure 4e). Despite a visible decrease in GPC (Figure 4d), GY increase (Figure 1) causes higher PY. The trend in PY is more visible under lowN.

Harvest index was increased over the period under lowN, but this relationship is not visible under highN (Figure 4f).

Grains per m<sup>2</sup> show an increase over time under both fertilization treatments, with a higher increase under highN (Figure 4h). Under lowN, the new cultivars tend to produce more grains per spike (Figure 4g).

## 4 | DISCUSSION

### 4.1 | Grain yield

For the present study, we took a deliberate choice to start our study with Runar, released in 1972, which marks the onset of the modern wheat cultivation era in Norway. Moreover, the older cultivars (cultivated before the 1970s) are substantially taller and more susceptible to lodging, which would have caused practical problems with the highN treatment without mechanically supporting the plants. The breeding period investigated is relatively short compared with many other studies of collections from regions with a long wheat cultivation history, including Ahrends et al. (2018), Akin et al. (2017), and Wu et al. (2014). The number of examined lines is, thus, relatively small, which limits statistical power to detect relationships.

The estimated annual genetic gains in GY for spring wheat in Norway since 1972 (on average 17.8 kg ha<sup>-1</sup>, 0.34%) show similarity to gains determined in numerous collections worldwide (Ahrends et al., 2018; Crespo-Herrera et al., 2017; Dube et al., 2019; Evans et al., 1980; Oury et al., 2012; Rodrigues et al., 2007; Voss-Fels et al., 2019; Woyann et al., 2019), although they are slightly lower. The gains being relatively small show that GY was not the only priority for breeders. Wheat breeding in Norway has put a great emphasis on baking quality (due to the fact that most of the production is used for breadmaking), disease resistance (e.g., powdery mildew, *Fusarium* head blight, septoria nodorum blotch), and resistance to lodging and preharvest sprouting (Lillemo & Dieseth, 2011). Fungal diseases as well as lodging and preharvest

sprouting are promoted by often rainy and windy weather during the season. The highest yielding cultivar, Arabella, is cultivated as a feed wheat due to its exceptional biomass and GY but does not meet the quality requirements for breadmaking in Norway.

The GY gains can be seen under both high and low fertilization inputs with similar cultivar ranking, showing that the source of improvement is of a genetic nature. The estimated gains are higher under high fertilizer input, which may indicate that the new cultivars are more responsive to increased N fertilization. This finding contradicts some of the results published (Ahrends et al., 2018), where the genetic progress relied strongly on the management applied (soil N availability). Our findings correspond to the results of Voss-Fels et al. (2019), where the progress was apparent across different management regimes. The new cultivars under low N input nearly approach the old ones under high input in terms of GY, which underlines genetic contribution to yield progress. Hypothesizing, it would be possible to reduce the fertilizer input by almost 50% and, by using new cultivars, still achieve yields close to those obtained with high input five decades ago. Despite the unrealistic nature of this scenario (constantly increasing national demand), it shows that breeding contributes to a more sustainable development of agriculture and leads to increased fertilizer use efficiency. This aspect is even more pronounced considering the higher PYs achieved by the newer cultivars. Based on our results, there are no apparent signs of the genetic gains approaching a plateau phase (Grassini et al., 2013).

### 4.2 | Agronomical and physiological traits

None of the investigated traits exhibited significant  $g \times m$  interaction (at 95% confidence level), and similar findings can be found in the literature (Geren et al., 2019; Mandic et al., 2015). The small cultivar pool investigated and use of the split plot design to maximize cultivar comparisons within fertilization level leaves little statistical power to assess the minor  $g \times m$  interactions that might be present. Increased fertilizer input has a positive influence on GY, PH, GPC, GF, DM, TKW, TW, GPC, PY, BM, grains per spike, and grains per area. Those results are in line with previous works (Amer, 2017; Asghar Ali et al., 2000; Mandic et al., 2015; Pradhan et al., 2018; Yu et al., 2018) and confirm the current view on fertilizer effects on crops.

### 4.3 | Grain yield and traits over the 1972–2019 period

The strong negative relation of GY and GPC, present under both fertilization rates, corresponds with the common view, for instance, of Monaghan et al. (2001) and Yu et al. (2018).

The increase in GY is achieved by accumulating more starch in the kernels at a cost of protein content. However, despite the decline in GPC, a positive relation of grain PY with year of release is observed. The negative relationship between GY and GPC is especially pronounced in high-yielding cultivars grown in European countries. A number of explanations for this phenomena have been proposed, but none is universally accepted (Simmonds, 1995). Bread making quality is a paramount breeding goal in Norway as the bulk of the domestic wheat production is being used by industrial bakeries. Newly released cultivars must be at least as good as cultivars already on the market in terms of yield, disease resistance, and agronomic properties, and match with the requirements for the different quality classes defined by the industry. It is a common practice nowadays in Norway to apply split fertilization with about two-thirds of N applied at sowing and the remainder at the heading stage. The latter amount is adjusted according to the yield potential of a cultivar to secure sufficient GPC, and therefore, achieve satisfactory baking quality. The trend observed in our data might be due to the fact that the highest-yielding cultivars have a higher grain set and the amount of N applied at sowing is not sufficient for them to reach their full potential in GPC. Grain protein content in wheat depends on the uptake of soil N before anthesis, its uptake during the GF, and finally, remobilization to grains of stored N in the plant. Larger N uptake before anthesis favors a higher grain number whereas late N uptake assures high GPC. It has been shown that up to 50% of total N in wheat plants at maturity may be taken up after anthesis (Austin et al., 1977; Ellen & Spiertz, 1980; Heitholt et al., 1990). Three of the cultivars present in our collection possess the wild-type allele of the *Gpc-B1* (*NAM-B1*) locus: Mirakel, Rabagast, and Polkka. The *Gpc-B1* wild-type allele is well documented to increase GPC, accelerate senescence, increase Fe and Zn content, and to reduce GY (Brevis & Dubcovsky, 2010; Uauy, Brevis, et al., 2006; Uauy, Distelfeld, et al., 2006). These three cultivars show no apparent difference in GPC, GY, and DM, showing that the general trend of decreasing GPC, delayed senescence, and increased GY was achieved by utilizing a larger number of small-effect quantitative trait loci rather than relying on a single, large effect locus.

Grain yield is strongly associated with DM. Longer GF results in an opportunity to gather more resources and allocate them in kernels, but this trait is difficult to balance under Norwegian growing conditions. Earliness is a desired trait as September (harvest time) is usually marked with frequent rainfall and wind, promoting lodging and preharvest sprouting. However, a shorter vegetative period comes with lower GYs and farmers in Norway must consider the balance between the possibility of growing later cultivars for higher yield with the risk of quality and yield loss due to difficult weather at the end of the season. Therefore, with the increase of latitude, earlier cultivars are desired in Norway due to the

shortening of the available growing season. Changing climate with increased growing season temperature over the past five decades has indeed allowed for the introduction of later-maturing cultivars as seen in the trend over years for DM. The spring in Norway arrived on average 7 d earlier in 2005 than in 1971 (Nordli et al., 2008), which aligns with our findings of an average 3 d longer time period between sowing and physiological maturity.

The relationship between grains per spike and grains per area was found to be a driver of yield gains in European wheat collections (Voss-Fels et al., 2019); however, this was not present among CIMMYT (Aisawi et al., 2015) nor Chinese (Yao et al., 2019) accessions. In our study, GY is correlated with the number of grains per spike and kernel weight (under low fertilization input), and with the number of grains per area (under high input), which aligns well with other studies on European wheat (Voss-Fels et al., 2019). However, in contrast to what has been shown for CIMMYT wheat (Aisawi et al., 2015), kernel weight shows no signs of consistent improvement in the 1972–2019 period; it is grains per area and grains per spike that exhibit such an increase. By that, we conclude that the yield progress in our collection is driven by the increase in grain number both per spike and area, considering also reports from other wheat collections in Europe.

Grain protein content showed a declining trend over the year of release in this study, which is connected to the progress in GY (reverse relationship between protein content and GY). This tendency, however, is more pronounced under the high N treatment, suggesting that the highest-yielding cultivars need more N to reach their protein content potential. Protein content of the older cultivars appear to be strongly responding to soil N availability. The newer cultivars also respond to fertilization; however, the GPC difference between the treatments is smaller than for the legacy cultivars.

Harvest index was slightly improved over the years in our collection, which is visible mostly under low fertilization. No trend was observed for biomass production of the cultivars under any treatment, which hints that GY increase is driven by HI improvement rather than increases in total biomass.

## 5 | CONCLUSIONS

Spring wheat breeding progress represented by a collection of 21 cultivars released in Norway during the past five decades increased the average GY by 17.8 kg ha<sup>-1</sup> (0.34%) per year under Norwegian growing conditions. Highly significant gains are present under both high and low fertilization treatments, providing grounds to conclude that breeding progress does not depend on intensive management. Increased fertilization has a significant positive effect on GY, PH, GPC, BM, grains per spike, TKW, TW, HI, and DM. Days to heading

and number of spikes per area are the only traits unaffected by fertilization. None of the traits were subject to a significant ( $\alpha = .05$ )  $g \times m$  interaction. Grain yield in the collection is associated mostly with number of grains per spike and number of grains per area. Breeding led to a development of later-maturing cultivars with prolonged GF, producing more grains per spike and grains per area. Grain yield gains have been driven mostly by prolonged GF and increasing the number of kernels per spike and number of kernels per area.

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## AUTHOR CONTRIBUTIONS

Tomasz Mróz: Data curation; Formal analysis; Investigation; Methodology; Visualization; Writing – original draft. Jon Arne Dieseth: Conceptualization; Supervision; Writing – review & editing. Morten Lillemo: Conceptualization; Funding acquisition; Project administration; Supervision; Writing – review & editing.

## CONFLICT OF INTEREST

Authors declare no conflicts of interest.

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