Original article
UDC 633.11:631.527
DOI: 10.30901/2227-8834-2023-3-21-31

Genetic gain of grain yield and quality in bread wheat cultivars representing 40 years of breeding in Morocco

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Background. Knowledge about the genetic gain for fundamental traits over time is essential for a critical assessment and improvement of breeding programs, especially regarding staple crops like bread wheat.
Materials and methods. To estimate the genetic gain in bread wheat breeding in Morocco, grain yield (GY) and grain protein content (GPC) data were collected from 12 multi-environment field trials for 20 bread wheat cultivars released between 1980 and 2022.
Results and discussion. Analysis of variance highlighted a high significant variability between environments (E), cultivars (G), and a significant G × E interaction ($P < 0.001$). Based on stability analysis, the modern cultivars released during the two last decades (2002–2012 and 2013–2022) showed the highest performances and wider stability than old ones, especially in low-yielding environments. Genetic gain (GG) for GY was 21.4 kg ha^{-1} yr^{-1} (0.75% yr^{-1}) over 4 decades of breeding. This progress was declining when advancing in decades and ranged from 11% (from 1980–1990 to 1991–2001) to less than 7% (from 2002–2012 to 2013–2022). The GG in low and intermediate yielding environments were the most important (17.34% and 6.88% yr^{-1} respectively), while GG was nonsignificant in high-yielding environments (4.62% yr^{-1}). Within the same period, GPC showed a nonsignificant negative trend of –0.007% (–0.002% yr^{-1}), while derivative parameters from GY and GPC indicated high positive genetic progress. More efforts should be deployed to implement a good balance between yield performance and quality in the new released cultivars despite the negative correlation between these two traits ($r = -0.36$; $P < 0.001$).
Conclusion. Adopting advanced technologies, like genomic selection, adequate agronomic practices, and more efficient selection criteria are essential steps to further increase simultaneously grain yield and quality traits.

Keywords: bread wheat, stability analysis, grain yield, grain protein content

Acknowledgements: this work could not have been accomplished without the contribution of the technical staff of all experiment stations at INRA.
The authors thank the reviewers for their contribution to the peer review of this work.

For citation: Bennani S., Taghouti M., Gaboun F. Genetic gain of grain yield and quality in bread wheat cultivars representing 40 years of breeding in Morocco. *Proceedings on Applied Botany, Genetics and Breeding.* 2023;184(3):21-31. DOI: 10.30901/2227-8834-2023-3-21-31

Научная статья
DOI: 10.30901/2227-8834-2023-3-21-31

Генетическое улучшение показателей урожайности и качества зерна у сортов мягкой пшеницы, созданных в Марокко за 40 лет селекции

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Актуальность. Анализ наследственных изменений важнейших агрономических показателей в определенные периоды необходим для оценки и улучшения селекционных программ основных культур, включая мягкую пшеницу.
Материалы и методы. Для оценки генетического эффекта селекции в Марокко получены и проанализированы данные по урожайности (GY) и содержанию белка в зерне (GPC) у 20 сортов мягкой пшеницы, созданных в период с 1980 по 2022 г., при выращивании в поле в 12 пунктах.
Результаты и обсуждение. Дисперсинный анализ показал высокозначимое влияние на изучаемые показатели факторов среды (E), генотипа (G) и значимое влияние их взаимодействия G × E (P < 0,001). По результатам анализа стабильности созданные за два последних десятилетия (2002–2012 и 2013–2022 гг.) сорта характеризуется наивысшими показателями изучаемых признаков и их большей стабильностью по сравнению с ранее созданными сортами, особенно в неурожайные годы. За 40 лет генетический эффект (GG) для урожайности семян (GY) составил 21,4 кг/га за каждый год (0,75% в год). Этот эффект со временем снижался, варьируя в пределах от 11% (с 1980–1990 по 1991–2001 гг.) до менее чем 7% (с 2002–2012 по 2013–2022 гг.). Генетический эффект в низко- и среднеурожайных условиях был наиболее выражен (17,34% и 6,88% за год соответственно) и оказался незначимым в высокоурожайных условиях (4,62% за год). За тот же период показатель GPC показал статистически незначимое снижение: –0,007% (–0,002% за год), в то время как показатели, производные от GY и GPC, указывали на высокий положительный генетический эффект селекции. Следует приложить больше усилий для достижения хорошего баланса между урожайностью и качеством семян новых сортов, учитывая отрицательную корреляцию между этими двумя признаками (r = –0,36; P < 0,001).
Заключение. Внедрение передовых технологий, таких как геномная селекция, соответствующая агротехника и более эффективные критерии отбора способны в будущем обеспечить одновременное повышение урожайности зерна и его качества.

Ключевые слова: мягкая пшеница, анализ стабильности, генетический эффект, урожайность, содержание белка в зерне

Благодарности: настоящая работа реализована благодаря тому вкладу, который внесли технические сотрудники всех опытных станций ИНРА.
Авторы благодарят рецензентов за их вклад в экспертную оценку этой работы.

Для цитирования: Беннани С., Тагути М., Габун Ф. Генетическое улучшение показателей урожайности и качества зерна у сортов мягкой пшеницы, созданных в Марокко за 40 лет селекции. *Труды по прикладной ботанике, генетике и селекции*. 2023;184(3):21-31. DOI: 10.30901/2227-8834-2023-3-21-31

Introduction

Bread wheat (*Triticum aestivum* L.) is one of the most important staple food crops worldwide, playing a major role in food security. Wheat production is facing many challenges due to increased competition for arable land, depleting natural resources, degrading soil health, biotic and abiotic stresses, and has to be increased at an annual rate of 1.3% per year to feed 9 billion of the world's population by 2050 (Woyann et al., 2019).

The release of high-yielding and climate-resilient cultivars of appropriate quality has been the most efficient approach to meet these challenges. Although wheat breeding has experienced dramatic improvement during the last century thanks to new technological advances, yield growth has been slowing more recently and has reduced from 2.19% per year for the period 1960–1990 to 1.07 from 1990 to 2010, and it is expected to be further reduced to 0.62 for the period 2010–2050 (Rife et al., 2019; Woyann et al., 2019). Grain protein content (GPC) is another staple trait for consumers and industrials determining the end-use properties of wheat, as well as the nutritional value of derived products (Giancaspro et al., 2019). Grain yield and protein content are complex quantitative traits, making selection a major challenge in wheat breeding because of the large "genotype × environment" interaction and the negative relationship between these two primary traits (Iqbal et al., 2016; Giancaspro et al., 2019).

While the adoption of technological advances helps to achieve breeding objectives, it is of fundamental importance to determine and track the amount of genetic progress that has been made in a breeding program so that new processes and breeding techniques can be adopted to cover future demands (Woyann et al., 2019). Genetic gain can be defined as the increase in average performance through genetic improvement after the environmental effect is excluded (Woyann et al., 2019). Most studies about public plant breeding programs efficiency reported genetic gains for wheat grain yield under 1% over the last 30 years (Cobb et al., 2019). For quality traits, few studies have been undertaken to assess their genetic progress and revealed mostly a nonsignificant gain or even a decline over time (Laidig et al., 2017; Hu et al., 2022).

In Morocco, bread wheat is highly consumed every day, mainly as bread, at an important rate of 200 kg/person/year. A limited number of studies have evaluated the rates of wheat genetic gains in drylands areas, such as Morocco, especially under the current environmental challenges, and so far, there has not been a study on the breeding progress for grain quality of bread wheat cultivars in Morocco. The objectives of the present work were to (I) determine the performance and stability of grain yield and quality of genotypes released over the 4 last decades from 1980 to 2022, and (II) quantify breeding progress over the main periods of release of bread wheat genotypes in the public breeding program in Morocco to propose an efficient breeding strategy and promote sustainable agriculture.

Materials and methods

1. Genetic material and field trials

In this study, a total of 20 bread wheat lines and cultivars spanning four decades of breeding from 1980 to 2022 at the National Institute of Agricultural Research (INRA) were evaluated under 12 Moroccan environments representative of the main bread wheat growing areas in Morocco. Genotypes were classified into 4 groups (decades) according to the year of release. A total of 4, 6, 2 and 8 lines/cultivars were respectively assigned to the decades 1980–1990, 1991–2001, 2001–2012, and 2013–2022. The last group comprises the latest registered cultivars in addition to the elite lines submitted for release. The full list is displayed in Table 1.

A randomized block design of three replications was used as the experimental design. Each entry was planted in plots of 6 m^2 at six experiment stations over the three seasons 2017, 2018, and 2020 in Morocco, for a total of 12 environments (sites × seasons). Planting was conducted between the 1st and the 10th of December. Agronomic management was performed according to recommended local practices at each location. None of the trials was subjected to insecticide or fungicide treatment to assess the genotypic performances and behavior under real environmental conditions.

Table 1. List of the 20 cultivars and elite lines of bread wheat used in the study and their year of release

Таблица 1. Список 20 сортов и элитных линий мягкой пшеницы, находившихся в изучении, и годы их создания

Cultivar/Line	Year of release	Decade of release
Marchouch	1984	1980–1990
Kanz	1987	1980–1990
Achtar	1988	1980–1990
Tilila	1989	1980–1990
Massira	1992	1991–2001
Amal	1993	1991–2001
Mehdia	1993	1991–2001
Rajae	1993	1991–2001
Arrehane	1996	1991–2001
Aguilal	1996	1991–2001

Cultivar/Line	Year of release	Decade of release
Kharroba	2010	2002–2012
Khadija	2012	2002–2012
Malika	2016	2013–2022
Snina	2017	2013–2022
Lina	2020	2013–2022
BT175	2022	2013–2022
BT155	Under submission	2013–2022
AV04	Under submission	2013–2022
AV21	Under submission	2013–2022
BTG	Under submission	2013–2022

2. Climatic conditions of cropping seasons

The 2017 /2018 cropping season showed regularity and good distribution of rainfall in space and time, despite the late arrival of the autumn rains. The 2018/2019 and 2019/2020 seasons were characterized by restrictive rainfall, poorly distributed during the crop cycle (Table 2).

within and across environments per decade. The genetic gain per year was then measured by dividing this value by 10 (years). The Pearson correlation analysis was used to highlight the relationships between all the studied traits, and decades. All those analyses were performed using the Genstat software (18th edition).

Table 2. Description of environments and experiment sites used for field evaluation

Таблица 2. Погодные условия и пункты проведения полевого изучения

Environment	Coordinates	Mean rainfall* (mm)	T min*	T max*	Cropping season	Rainfall (mm)
Allal Tazi (AT18)	34°31' N / 6°19' W	514	5	33	2017–2018	274
Allal Tazi (AT19)					2018–2019	139
Allal Tazi (AT20)					2019–2020	349
Douyet (DYT18)	34°00' N / 5°00' W	410	5	31	2017–2018	426
Douyet (DYT19)					2018–2019	318
Marchouch (MCH18)	33°34'3.1" N / 6°38'0.1" W	375	7	32	2017–2018	512
Marchouch (MCH19)					2018–2019	113
Marchouch (MCH20)					2019–2020	354
Sidi El Aidi (SEA18)	33°9'36" N / 7°24'0" W	300	1	43	2017–2018	305
Sidi El Aidi (SEA20)					2019–2020	199
Jemaat Shaim (JSH18)	32°40' N / 10°0' W A	256	8	35	2017–2018	232
Khemiss Zemamra (KHZ18)	32°37' N / 8°42' W	250	12	28	2017–2018	340

* – Annual average rainfall and temperature during the last five cropping seasons
* – Среднегодовая сумма осадков и температура за последние пять вегетационных периодов

Rainfall was highly correlated with yield performance (r = 0.70; P = 0.011), while a nonsignificant correlation linked rainfall to GPC (r = 0.09; P = 0.77). The environments were categorized depending on their yield performance in three groups: low-yielding environments (< 2 t ha^{-1}); intermediate yielding environments (> 2 and < 4 t ha^{-1}) and high-yielding environments (> 4 t ha^{-1}).

3. Trait measurements and statistical analysis

Grain yield (GY) was driven from 4.5 m^2 of harvested plot and converted to the standard unit of metric ton per hectare (t/ha). Grain protein content (GPC) was assessed using an infraneo NIR grain analyzer as a percentage of dry weight (% DW).

At the first stage, an analysis of variance (ANOVA) was performed for each trait and environment independently using the SAS software. Then, a combined analysis of variance was carried out to assess the effects of the genotype, environment, and genotype × environment. Significant differences at the 5% confidence limit were identified by the Bonferroni mean comparison. Based on mean data, the AMMI analysis (Yan et al., 2000) and superiority index (Pi) calculation (Lin, Binns, 1988) were used for the stability and adaptability analysis. Grain-yield protein (GYP) was calculated for each environment as the product of GPC and GY and corresponded to the grain protein harvested per area (Koekemoer et al., 1999). The absolute (AGG, trait unit/time unit) and relative genetic gain (RGG, %/time unit) were calculated for all traits. A regression analysis, with a standard linear model applied to decade cultivar means, was used to calculate rates of change

Results

1. Field trials – Combined and individual analyses of variance

The combined ANOVA showed very highly significant differences between environments, genotypes, and environment × genotype interactions for both grain yield (GY) and grain protein content (GPC) (P < 0.001). The environmental component was the predominant source of variation, accounting for 87% and 90% of the total sum of squares of GY and GPC, respectively, while the genotypic effect was almost four times that of the genotype × environment interaction (2 and 1% respectively) (data not shown). The average GY and GPC were respectively 2.98 t ha^{-1} and 14.24% DW across all 12 environments. The newly submitted lines BTA21 (4.41 t ha^{-1}), BTA04 (4.31 t ha^{-1}), and BTG (3.90 t ha^{-1}) presented the highest mean GY values, while the least performances were manifested by the old cvs. 'Kanz' (2.28 t ha^{-1}), 'Rajae' (2.55 t ha^{-1}), 'Marchouch' (2.67 t ha^{-1}), and 'Tilila' (2.68 t ha^{-1}). Regarding quality, cv. 'Marchouch' had the highest mean value of GPC (15.3%), followed by 'Massira' (15.1%), 'BT155' (15.2%), and 'Kharouba' (15.1%), whereas the lowest values were attributed to the new lines BTA04 (11%), BTA21 (11.1%), and BTG (12%) (Table 3).

The combined ANOVA revealed highly significant differences between groups in terms of GY, and nonsignificant differences for GPC. The groups 2013–2022 (3.19 t ha^{-1}) and 2002–2012 (2.98 t ha^{-1}) showed the highest performances in terms of GY (Table 3). The one-way ANOVA showed signifi-

Table 3. Grain yield (GY, t ha^{-1}), and grain protein content (GPC, % DW) of bread wheat cultivars and elite lines, and the corresponding superiority index (Pi)

Таблица 3. Урожайность зерна (GY, т/га), содержание белка зерна (GPC, %) у сортов и элитных линий мягкой пшеницы и соответствующие индексы превосходства (Pi)

Cultivar/Line/ Decade	Combined data		Low-yielding environments		High-yielding environments		Intermediate yielding environments	
	GY (Pi)	GPC (Pi)	GY (Pi)	GPC (Pi)	GY (Pi)	GPC (Pi)	GY (Pi)	GPC (Pi)
Marchouch	2.66 (1.45)	15.28 (0.84)	1.05 (0.69)	16.57 (0.29)	4.32 (2.62)	15.64 (2.33)	2.97 (1.37)	14.03 (0.39)
Kanz	2.29 (2.98)	14.34 (2.63)	1.03 (0.75)	15.07 (2.92)	3.12 (7.38)	15.45 (3.24)	2.79 (2.11)	13.08 (2.03)
Achtar	2.78 (1.51)	13.74 (3.54)	0.98 (0.81)	15.15 (2.45)	5.13 (1.67)	14.34 (4.99)	2.86 (1.97)	12.25 (3.54)
Tilila	2.68 (1.54)	13.84 (3.18)	0.93 (0.86)	14.55 (3.56)	4.07 (3.07)	14.16 (5.22)	3.23 (1.16)	13.09 (1.66)
Massira	2.74 (2.69)	15.14 (1.34)	1.70 (0.17)	16.38 (0.67)	3.90 (7.44)	15.91 (2.81)	2.87 (1.85)	13.68 (0.98)
Amal	2.79 (1.34)	13.63 (4.53)	1.25 (0.48)	15.12 (2.16)	4.68 (2.31)	13.42 (9.13)	2.90 (1.45)	12.56 (3.66)
Mehdia	2.95 (0.99)	13.86 (3.62)	1.19 (0.55)	15.76 (1.27)	4.87 (1.41)	13.99 (7.39)	3.21 (1.11)	12.26 (3.24)
Rajae	2.55 (1.51)	13.45 (4.45)	0.73 (1.12)	14.16 (6.02)	4.44 (2.07)	14.43 (4.60)	2.88 (1.49)	12.30 (3.09)
Arrehane	3.09 (0.78)	14.29 (2.55)	1.49 (0.30)	15.51 (1.52)	4.92 (1.26)	14.76 (5.06)	3.27 (0.88)	13.04 (1.86)
Aguilal	2.87 (1.23)	12.86 (6.53)	1.15 (0.61)	13.83 (5.48)	5.42 (0.73)	12.81 (11.7)	2.73 (2.02)	12.11 (4.25)
Kharroba	2.77 (1.76)	15.08 (0.96)	1.07 (0.65)	16.64 (0.15)	3.39 (5.55)	16.59 (0.43)	3.75 (0.38)	12.92 (1.91)
Khadija	3.16 (0.70)	14.35 (2.59)	1.54 (0.34)	15.68 (1.28)	5.34 (0.68)	14.69 (5.41)	3.14 (1.00)	13.07 (1.97)
Malika	2.97 (1.02)	14.51 (1.87)	1.73 (0.13)	15.57 (1.25)	4.72 (1.58)	15.22 (3.58)	2.90 (1.38)	13.23 (1.34)
Snina	3.04 (1.32)	14.51 (2.08)	1.79 (0.09)	15.37 (1.75)	4.96 (1.99)	14.92 (4.47)	2.88 (1.90)	13.59 (0.93)
Lina	3.35 (0.09)	14.46 (2.52)	1.55 (0.19)	16.80 (0.52)	5.46 (0.00)	12.00 (10.8)	4.99 (0.00)	12.18 (1.39)
BT175	3.28 (0.11)	13.96 (3.06)	2.07 (0.00)	16.08 (1.02)	4.85 (0.18)	12.15 (10.1)	4.28 (0.25)	11.70 (2.58)
BT155	2.82 (0.38)	14.68 (2.12)	1.43 (0.21)	17.06 (0.21)	5.14 (0.05)	12.25 (9.68)	3.75 (0.79)	12.32 (1.21)
BTA04	4.31 (0.43)	10.95 (7.78)	–	–	5.12 (0.06)	10.9 (16.5)	3.89 (0.61)	10.97 (3.41)
BTA21	4.41 (0.33)	11.13 (6.98)	–	–	5.18 (0.04)	11.45 (13.5)	4.02 (0.48)	10.98 (3.72)
BTG	3.91 (1.17)	11.70 (5.15)	–	–	4.64 (0.34)	11.7 (12.3)	3.54 (1.59)	11.70 (1.60)
1980–1990	2.60 (0.47)	14.32 (0.41)	0.99 (0.34)	15.34 (0.84)	4.16 (0.55)	14.90 (0.51)	2.96 (0.41)	13.11 (0.06)
1991–2001	2.88 (0.25)	13.73 (1.06)	1.25 (0.15)	15.13 (0.83)	4.71 (0.11)	14.22 (1.61)	2.97 (0.38)	12.66 (0.29)
2002–2012	2.98 (0.23)	14.71 (0.09)	1.30 (0.15)	16.16 (0.01)	4.36 (0.62)	15.64 (0.07)	3.45 (0.02)	12.99 (0.12)
2013–2022	3.19 (0.14)	14.54 (0.23)	1.72 (0.00)	16.09 (0.10)	4.96 (0.01)	13.40 (0.79)	3.54 (0.27)	12.44 (0.03)

cant to very highly significant differences between decades for GY under all the environments, except DYT18, KHZ18 and SEA18. The quality trait presented less variability within each environment between genotypes and groups. The highest GPC value belonged to the group 2002–2012, with 14.7%, instead of a mean value of 14.3% for the other groups (see Table 3).

2. Stability analysis

The GGE analysis showed a number of intercrossings between environments, making difficult to generate independent megaenvironments (Figure).

Based on the superiority index (Pi), the lowest value corresponded to the decade 2013–2022, showing dynamic stability and high performance (3.2 $t\ ha^{-1}$; Pi = 0.135) over environments. The new cvs. 'Lina', 'BT175', and 'BTA21' exhibited the lowest values of Pi, ranging from 0.097 to 0.331, and were among the highest-yielding cultivars varying from 3.3 to 4.4 $t\ ha^{-1}$. For GPC, the group 2002–2012 was the best performing (14.71% DW) and stable (Pi = 0.096), followed by 2013–2022 (14.54% DW; Pi = 0.229). Cvs. 'Marchouch', 'Kharroba', and 'Massira' showed the lowest values of Pi, ranging from 0.842 to 1.337, and GPC values from 15.08 to 15.28% DW (see Table 3).

When evaluating performances across different types of environments, the group 2013–2022 was the most stable and the highest-performing under low-yielding environments in terms of GY (Pi = 0.007; GY = 1.72 $t\ ha^{-1}$); while it ranked second in terms of quality (Pi = 0.10; GPC = 16.09% DW) after the group 2002–2012. Cvs. 'BT175', 'Snina' and 'Malika' presented stable (0 > Pi > 0.13) and high yields, ranging from 1.73 to 2.07 $t\ ha^{-1}$. These cultivars also expressed a good level of GPC, ranging from 15.37 to 16.08% DW, in comparison with 'Kharroba', 'BT155' and 'Marchouch' (16.57 > GPC > 17.06% DW). Under intermediate yielding environments, the groups 2002–2012, followed by 2013–2022, manifested the highest yields (3.45 and 3.54 $t\ ha^{-1}$, respectively) and the lowest Pi values (0.02 and 0.27, respectively). These groups expressed also the best quality performances: 12.99% DW (Pi = 0.12), and 12.44 (Pi = 0.03). The lines Lina, BT175 and Kharroba were the best stable (0.0 > Pi > 0.38) and high-yielding genotypes, ranging from 3.75 and 4.99 $t\ ha^{-1}$; while their GPC values ranged from 12.18 to 12.92% DW. The highest-performing cultivars in terms of quality were 'Marchouch', 'Snina' and 'Massira', with the lowest Pi values and the highest GPC values (13.59–14.03% DW). Finally, for high-yielding environments, the group 2013–2022 was the most stable and the most high-yielding group (GY = 4.96 $t\ ha^{-1}$; Pi = 0.013), while it recorded a mean GPC value of only 13.40% DW. The new Lina, BT155, BTA04 and BTG lines were the most stable, with Pi values ranging from 0 to 0.06 and GY varying from 5.12 to 5.46 $t\ ha^{-1}$. For GPC, 'Kharroba' was the best cultivar in terms of GPC and stability (GPC = 16.59; Pi = 0.43) (see Table 3).

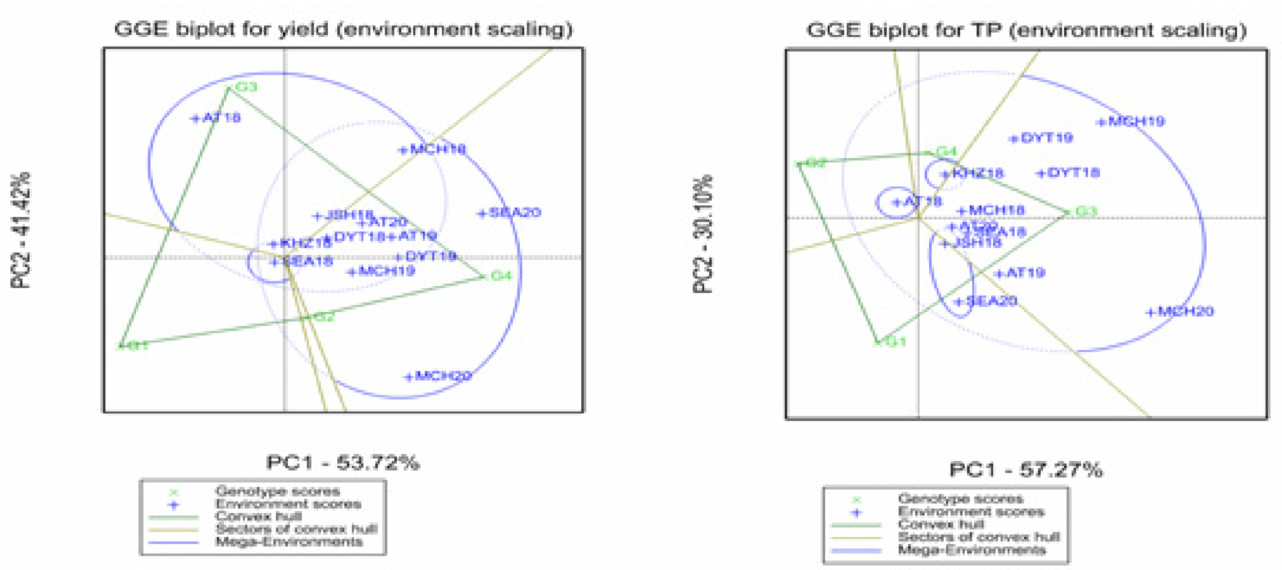

Figure. GGE analysis per decade of release for grain yield and protein content

Рисунок. Анализ факторов «генотип» и «генотип × среда» для урожайности и содержания белка по годам создания сортов/линий

3. Genetic gain of grain yield

A combined analysis across environments showed a decade-wise GG for GY of 21.4 $kg\ yr^{-1}$, corresponding to 0.75%/year, with about 28% of yield increase through four decades of breeding efforts. A vast majority (8) of the environments had significant GG for GY, with genetic gains varying from 16.7 $kg\ ha^{-1}\ yr^{-1}$ at MCH19 (1.33% yr^{-1}) to more than 71 $kg\ ha^{-1}\ yr^{-1}$ (1.39% yr^{-1}) at MCH18 (Table 4).

When evaluating within types of environments, the low-yielding ones showed the most significant and highest genetic gain of 22.84 $kg\ ha^{-1}\ yr^{-1}$ (1.73% yr^{-1}) compared to intermediate yielding (21.88 $kg\ ha^{-1}\ yr^{-1}$; 0.69% yr^{-1}) and high yielding environments (21.2 $kg\ ha^{-1}\ yr^{-1}$; 0.46% yr^{-1}) (see Table 4). The genetic gain for high-yielding environments was nonsignificant (P = 0.208).

When comparing the individual genetic gain from a group to another, the results of regression analysis showed an obvious advantage of the group 1991–2001 compared to the group 1980–1990 with a positive significant slope of b = 1.05 and a nonsignificant constant a = 0.16 corresponding to an average yield increase of 11%, varying from 29 up to 93 $kg\ ha^{-1}$. The progress is less apparent from 1991–2001 to 2002–2012, with a highly significant slope (b = 0.96) and a positive nonsignificant constant (a = 0.17), and an average gain of 2.4%. The slope of regression from 2002–2012 to 2013–2022 was much less important but highly significant (b = 0.76), while the constant was nonsignificant (a = 0.92), with an average gain of 7.2%.

Table 4. Absolute and relative genetic gain for GY, GPC, and GYP

Таблица 4. Абсолютные и относительные показатели генетического эффекта для урожайности зерна, содержания белка в зерне и сбора белка с единицы площади

Environments	Absolute genetic gain						Relative genetic gain (% yr^{-1})	
	GY (kg ha^{-1} yr^{-1})		GPC content (% yr^{-1})		GYP (kg ha^{-1} % DW)		GY	GPC
	Fpr	GG	Fpr	GG	Fpr	GG		
AT18	0.349	22.5	0.829	–0.005	0.552	140	0.69	–0.039
DYT18	0.717	21.1	0.338	0.043	0.474	487	0.51	0.23
JSH18	0.016	21.6	0.648	–0.014	0.037	217	1.26	–0.096
KHZ18	0.757	3.6	0.302	0.031	0.333	117	0.17	0.22
MCH18	0.003	71.0	0.699	0.00+	0.003	788	1.39	0.06
SEA18	0.347	–5.42	0.533	–0.013	0.369	-85	–0.16	–0.09
AT19	< 001	32.5	0.742	–0.004	< 0.001	397.5	2.07	–0.035
DYT19	< 001	32.4	0.009	0.032	< 0.001	586.2	3.81	0.18
MCH19	0.001	16.7	< 001	0.069	< 0.001	391.2	1.33	0.38
AT20	0.012	27.1	0.386	0.01	0.005	375	0. 80	0.08
MCH20	0.036	21.8	0.648	–0.010	0.088	211	0.47	–0.08
SEA20	0.001	54.4	0.644	0.009	0.003	276	1.59	0.05
Low-yielding environments	< 0.001	22.84	0.330	0.326	< 0.001	377	1.73	0.21
Intermediate yielding environments	0.005	21.88	0.266	–0.177	0.001	277.5	0.69	–0.14
High-yielding environments	0.208	21.20	0.281	–0.367	0.44	147	0.46	–0.26
Combined data	0.001	21.40	0.950	–0.0007	0.003	276.4	0.75	–0.002

4. Genetic gain of grain protein content and grain yield protein

The evolution for GPC remained stable and nonsignificant (0.0007% DW yr^{-1}; $P = 0.950$) from 1980–1990 to 2013–2022, regardless of the environment type. Only 2 out of 12 environments (MCH19 and DYT19) manifested significant GG with 0.07% DW yr^{-1} and 0.032% yr^{-1}, respectively (see Table 4).

The results showed a highly positive significant negative trend of GYP (276 kg ha^{-1} % DW yr^{-1}) over time per decade. Considering each type of environments, there was a highly significant progress especially under low-yielding environments ($P < 0.001$) and to a lesser extent under intermediate yielding environments; while high-yielding environments showed a nonsignificant progress over time ($P > 0.05$) (see Table 4).

5. Relationship between protein content, grain yield, and derivatives

Overall, a highly significant negative correlation linked GY and GPC (r = –0.36 ; $P < 0.001$). The regression analysis of GPC on GY showed a negative slope (b = –0.587) with a coefficient of determination of 0.12. Regarding the types of environments, there was a significant negative correlation between GPC and GY under high-yielding (r = –0.384; $P < 0.001$), intermediate (r = –0.325; $P < 0.001$); and low-yielding environments (r = –0.351; $P < 0.001$).

The correlation analysis showed a highly significant relationship between GY and decades of release (r = 0.14; $P < 0.001$). Within the types of environments, this correlation was significant for intermediate (r = 0.281; $P < 0.001$) and low-yielding environments (r = 0.407; $P < 0.001$); while it was nonsignificant for high-yielding environments (r = 0.151; $P = 0.11$). The correlation analysis showed a nonsignificant positive association between GPC and the four decades of release (r = 0.013 ; $P = 0.779$). The correlation between GPC and decades was weakly significant under intermediate (r = –0.142; $P = 0.045$) and low-yielding environments (r = –0.165; $P = 0.034$); while it was nonsignificant for high yielding environments (r = –0.147; $P = 0.119$).

The correlation between GY and GYP was the most important (r = 0.948; $P < 0.001$); with Pearson values ranging from 0.88 ($P < 0.001$) for high-yielding environments, 0.89 ($P < 0.001$) for low-yielding environments, to 0.92 ($P < 0.001$) for intermediate yielding environments.

Discussion

Grain yield (GY) and grain protein content (GPC) are critical traits in wheat breeding programs, determining the economic value of this crop worldwide and the nutritional value of derived products. The aim of this research was to evaluate the genetic gain of GY and GPC in 20 bread wheat cultivars released during four decades of breeding in Morocco from 1980 to 2022 in order to improve the efficiency of breeding strategies.

1. Genotype, environment, and genotype × environment effects

The analysis of variance showed highly significant differences between environments (E) and genotypes (G), with a highly significant G × E interaction for grain yield (GY) and grain protein content (GPC). The environmental component explained the highest portion of the total source of variation (> 80%). This result reflects the diversity of contrasted multilocational agroclimatic conditions in terms of biotic and abiotic stress intensity and occurrence, and their influence on the performance and ranking of genotypes (Guzmán et al., 2016; Bassi, Sanchez-Garcia, 2017; Giancaspro et al., 2019; Woyann et al., 2019). In Morocco, rainfall is the main environmental driver of genotypic performances (Jlibene, 2011), as supported by the correlation between yield and rainfall data. Genotypic effect was also significant for GY and GPC in most of environments, showing that cultivars react differently to water restrictions. Multilocational data and stability analysis demonstrated the superiority of the lines released during the period of 2013–2022, especially Lina and BT175, which combined high yield, better yield stability, and adequate protein content across all types of environments. Therefore, modern cultivars had both improved yield potential and tolerance to moisture stress, resulting in an overall higher and stable grain yield and more responsiveness to environmental changes. On the other hand, the cultivars released during the 2002–2012 decade demonstrated the highest GPC values with the best stability across environments. Most of the new cultivars recently released or under registration process from 2020 to 2022 incorporated genes from wild species like *Aegilops squarrosa*, resulting in longer spikes and higher 1000 kernel weight. Wheat progenitors constitute a wide gene pool for relevant climate-responsive traits (Leigh et al., 2022).

2. Genetic gains for grain yield

The wheat yield exhibited a continuous positive increase: from 2.57 t ha^{-1} in 1980–1990 to 3.28 t ha^{-1} in 2013–2022. This means that the new released cultivars are a key for improving yields, especially that more than half of the test environments used for the analysis faced severe to moderate drought (Hu et al., 2022). The significant average annual genetic gain (GG) in GY since 1980 was found to be 21.4 kg yr^{-1} (0.75%/year), establishing the efficient contribution of breeding activities carried out in the last four decades towards improving the wheat yields in Morocco. M. Jlibene (2011) reported a lower mean genetic gain of 17 kg yr^{-1} using a set of Moroccan cultivars released from 1973 to 2006 and evaluated in 19 environments, varying from 13 kg yr^{-1} in rainfed unfavorable areas to 22 kg yr^{-1} in rainfed favorable environments. The GG obtained was within the range reported in Spain (0.88% yr^{-1} from 1931 to 2000) (Sanchez-Garcia et al., 2013), and France (0.66% yr^{-1} from 1962 to 1988) (Brancourt-Hulmel et al., 2003). Other studies reported higher values of GG, ranging from 1.1% yr^{-1} in the United States Central Plains from 1903 to 2014 (Rife et al., 2019) to 1.17% yr^{-1} in Argentina from 1940 to 1999 (Lo Valvo et al., 2018) and 1.29% yr^{-1} in China during the period of 1950–2015 (Hu et al., 2022). J. N. Cobb et al. (2019) reported that most public wheat breeding programs realized less than 1% of GG over the last 30 years.

GY is a result of yield potential of cultivars and their response to a combination of several environmental stresses (Bassi, Sanchez-Garcia, 2017). Great differences between environments were noted in genetic gain rates. The highest GG was recorded for the driest Moroccan environments, reflecting the superiority of climate-resilient cultivars released recently, incorporating many efficient resistance genes against the main biotic and abiotic stresses. Furthermore, the annual genetic gain was significantly more important under low-yielding and intermediate environments (15.9% and 17.3% yr^{-1}, respectively); while it was nonsignificant for high-yielding environments (6.8% yr^{-1}). In Morocco, the drought frequency has risen to 5 or 6 events every 10 years since the beginning of the 21st century. Since the Mediterranean area has been identified as a hot spot of climate change, the most important wheat-producing regions are suffering continuously from increasing intensities of drought and heat. Therefore, low-yielding and intermediate environments, where this crop is mainly cultivated under a rainfed system, account for more than 85% of the whole wheat production in Morocco during the two last decades (Verner et al., 2018). Recently, the national bread wheat breeding program at the National Institute of Agricultural Research (INRA) has focused on enhancing yield stability through incorporating drought tolerance, and resistance to *Septoria tritici*, yellow rust, and the Hessian fly as major selection traits to overcome the current environmental challenges even at the expense of yield potential.

However, the progress from a decade to another highlighted the limited rate of gain from 2001–2012 to 2013–2022, indicating a trend toward a plateau or potential stagnation of genetic gain, resulting from the negative impact of climate change on wheat yields and the narrowed genetic diversity with the development of breeding (Woyann et al., 2019; Hu et al., 2022). This stagnation has been reported by several earlier studies (Lo Valvo et al., 2018; Woyann et al., 2019), and makes it more urgent to develop a more efficient breeding strategy.

3. Genetic gains for grain protein content

Regarding quality, the data set showed a nonsignificant negative linear regression for GPC and, therefore, a nonsignificant progress in Morocco from 1980 to 2022. The newly bred wheat cultivars have maintained stable protein concentration in the last 40 years. However, the 2002–2012 and 2013–2022 decades exhibited respectively the highest values (> 14% DW). According to the classification of wheat quality, all cultivars exhibited a medium (11 > GPC > 13.5% DW) or high (GPC > 13.5% DW) grade of protein content depending on the environment. This finding was in line with other studies which noted a slight deterioration or nonsignificant progress of quality traits (Laidig et al., 2017; Hu et al., 2022).

Wheat grain quality has received much less attention and is often overlooked in the efforts to improve yield (Hu et al., 2022). This stagnant progress may result from the significant increase in grain yield, which enhances starch accumulation in the wheat grain that accounts for approximately 70% of grain dry weight, and therefore dilutes other grain components, including protein (Hu et al., 2022). In fact, even if quality has been considered as an important selection trait in bread wheat breeding, affecting the nutritional quality and the end use value and baking properties of wheat flour, breeders struggled to combine high-yielding cultivars with a high grade of quality. Furthermore, premium prices are not applied for high-quality wheat, like in some developed countries, i.e., the U.S. and Canada, resulting in farmers' reluctance to lose a margin of their yield in favor of better quality (Tadesse et al., 2019).

4. Grain yield and grain quality relationships

The environmental component had different effects on the two studied traits. Severe drought had heavy negative impact on GY during dry seasons, contrary to GPC which reached its highest values under dry conditions, as stated by many researchers (Özturk, Aydin 2004; Bennani et al., 2018). Although the underlying reasons for this negative relationship is still ambiguous, N. G. Munier-Jolain and C. Salon (2005), and M. Bogard et al. (2010) explained this behavior through fertilization, nitrogen uptake, and the interrelationship between carbon and nitrogen metabolism at the canopy level. Contrary to wet conditions, yield response to available nitrogen is low under dry conditions, while high-protein grain is achieved easily with little or no nitrogen fertilizer. However, the importance of climatic factors, especially drought stress, may lessen nitrogen uptake on GPC and result in alteration of the bread wheat quality in response to the reduction in N accumulated (Bogard et al., 2010 ; Guzmán et al., 2016).

The correlation analysis confirmed the negative relationship between GY and GPC in low-yielding, intermediate and high-yielding environments, making difficult the simultaneous improvement of grain yields while maintaining a good level of protein content (Bogard et al., 2010; Laidig et al., 2017; Hu et al., 2022). This finding is in line with many research studies (Oury, Godin, 2007; Iqbal et al., 2016; Geyer et al., 2022) and is explained by the multiple genes controlling these complex traits and the interactions that each gene has with the environmental component (Bassi, Sanchez-Garcia, 2017; Giancaspro et al., 2019). However, this relationship is not always true and depends on the environment reflecting the importance of genotype × environment interactions for GY and GPC that hide the GY/GPC relationship (Oury, Godin, 2007; Bogard et al., 2010).

In order to improve GY and GPC simultaneously, various methods were reported, including statistical parameters combining yield and protein. Grain-yield protein (GYP) was applied to better evaluate the GY/GPS relationship and to identify superior cultivars with the best balance between GY and GPC without concurrent reduction for any trait (Monaghan et al., 2001; Geyer et al., 2022). Our findings revealed significant genetic and environmental effects of this index, as stated by other studies (Monaghan et al., 2001; Oury, Godin, 2007). GPD showed a highly significant correlation with GY and GPC and the highest positive values for the genotypes released during the two last decades. These findings were in line with other studies (Koekemoer et al., 1999; Rapp et al., 2018).

5. Improvement of the breeding strategy to increase genetic gains

Taking into account the key findings of our study, several suggestions might help to improve the current breeding strategy for sustainable genetic improvement.

1. The substantial effect of climatic variables on the estimated GG and the stability results should drive the new breeding strategy to focus on specific adaptation through selecting elite stable lines for each megaenvironment (product profiles) in order to mitigate G × E interaction effects.

2. A significant improvement and progress have been achieved in Moroccan bread wheat productivity till now, while GPC remained relatively stable over time. Simultaneous improvement of both traits becomes pressing within the increasing of dry seasons in recent years to enhance consumers' income and living health standards (Giancaspro et al., 2019). J. Monaghan et al. (2001) and F. X. Oury and C. Godin (2007) suggest to undertake selection programs based mainly on GY, while at the same time adopting appropriate cropping practices for enhancing GPC, like zero tilling, water supply, and targeted N fertilization management, or selecting for increased efficiency in nitrogen partitioning in improved germplasm.

3. Improving the nutritional value of new cultivars may be realized through the use of wild germplasm which holds a high quality grade in comparison with common bread wheat cultivars. Advanced genetic tools such as speed breeding and genomics in line with high throughput phenotyping provide a more precise combination of beneficial traits and accelerate breeding gains in the field (Tadesse et al., 2019).

4. Strengthening networking at the national and international levels (CIMMYT and ICARDA) would help to have access to new technologies and a wide range of germplasm with higher yield potential and stability, and end-use qualities to reach farmers' and manufacturers' needs for a sustainable national wheat production.

5. Determining periodically the rate of genetic gain in key traits within breeding programs helps to adopt new processes and breeding techniques for better efficiency. Other yield components and quality traits should be assessed for their progress to better guide the selection of secondary traits and achieve more efficient simultaneous improvement.

Conclusion

The present study was aimed to measure the impact of more than 4 decades of the INRA bread wheat breeding program from 1980 to 2022. Huge environmental effects had a pressing impact on genetic gains. Great achievements have been made in grain yield improvement during the last four decades in Morocco, while there was no significant progress in protein content. The national breeding strategy should combine simultaneously better quality and enhanced genetic gains for yield in the new released cultivars through using advanced technologies, wild genetic resources and landraces, and incorporating adequate management practices like zero-till planting and targeted N fertilization management, combined with the product profile approach.

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Contribution of the authors: All authors contributed to the revision of this work critically for important intellectual content and editing. Bennani S. – data collection and interpretation; data analysis; writing the original draft of the manuscript. Taghouti M. – contribution to data interpretation. Gaboun F. – data analysis; contribution to data interpretation.
Вклад авторов: Все авторы внесли вклад в критическую проверку настоящей работы с целью повышения значимости интеллектуального содержания и редактирования. Беннани С. – сбор и интерпретация данных; анализ данных; написание первоначального варианта рукописи. Тагути М. – участие в интерпретации данных. Габун Ф. – анализ данных; участие в интерпретации данных.

Conflict of interests: the authors declare no conflicts of interests.
Конфликт интересов: авторы заявляют об отсутствии конфликта интересов.

The article was submitted on 23.12.2022; approved after reviewing on 10.05.2023; accepted for publication on 04.09.2023.
Статья поступила в редакцию 23.12.2022; одобрена после рецензирования 10.05.2023; принята к публикации 04.09.2023.