Genetic Improvement of Agronomic Traits of Winter Wheat Cultivars Released in France from 1946 to 1992

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ABSTRACT

In a context where agricultural practices in Europe are likely to go toward extensive systems with lower inputs, it is important to determine the genetic improvement of winter wheat (*Triticum aestivum* L.) not only in high-input agricultural systems but also in low-input systems. This study assesses the improvement in agronomic traits of winter wheat cultivars cultivated in France during the second half of the 20th century at four agronomic treatments: two levels of fungicide were combined with two levels of nitrogen fertilizer. Fourteen cultivars introduced between 1946 and 1992 were grown for two years (1994 and 1995) at five locations. Selection played a major role in the increase in winter wheat yield after 1946. The contribution of selection to this increase depended on the agronomic treatment and varied from one third to one half. Reduction of height was the most important factor. New cultivars with shorter straw expressed higher harvest index values and more consistent higher yields since they were less susceptible to lodging. The ability to produce more kernels from a given total above-ground biomass was the second factor. The number of kernels per unit area had increased over time without alteration of the weight of the kernels. The negative relationship between 1000-kernel weight and kernel number/m^2 was therefore shifted and new cultivars were thus able to fill more kernels than older entries. Modern cultivars used N more efficiently than their predecessors. The future challenge will be to obtain, in low-input systems, the same genetic gains as in high-input systems.

The yield of wheat increased very slowly in France during the 19th and early 20th centuries, from 0.9 Mg ha^{-1} in 1800 to 2.0 Mg ha^{-1} in 1950, with a gain of less than 10 kg ha^{-1} yr^{-1}. National yields increased more rapidly from 1956 to 1999 reaching 126 kg ha^{-1} yr^{-1} (Fig. 1). Despite climatic effects, the yield increase was linear over this period, and no significant decline has occurred in recent years.

Many authors have compared the yield potential of old and modern cultivars as reported by Slafer and Andrade (1991) and by Feil (1992). Most studies have been conducted in the USA, Australia, Mexico, and Western Europe (United Kingdom, Germany, France, Sweden). Their main objective was to determine the genetic gain measured in grain yield on the basis of data collected over a relatively long period from cultivar trials including check cultivars, or direct comparisons of old and modern cultivars grown simultaneously in trials conducted for that specific purpose. This second approach usually provides more directly comparable information, particularly about yield components. The main results of such studies are given in Table 1. Genetic gains for grain yield varied from 5.8 kg ha^{-1} yr^{-1} to 59 kg ha^{-1} yr^{-1}. Theses gains represent 33 to 63% of the national grain yield increase (Table 1).

The superiority of modern cultivars was mainly associated with higher kernels per square meter (KN). A few studies have shown either an increase in 1000-kernel weight (TKW) (Cox et al., 1988) or a decrease (Sinha et al., 1981; Waddington et al., 1986; Perry and d'Antuono, 1989). The increase in KN was mostly due to an increase in the number of kernels per spike (Hoeser et al., 1979; Slafer and Andrade, 1989), or due to increases in both kernels per spike and number of spikes per unit area (Sinha et al., 1981; Grignac et al., 1981; Ledent and Stoy 1988; Karpenstein-Machan and Scheffer, 1989; Austin and Ford, 1989; Perry and d'Antuono, 1989). Feil (1992) suggested that the stagnation of the mean TKW may be due to the fact that kernels added by breeding occur at sites in the spikelets that normally develop below average TKW values.

Increases in grain yield have been shown to be associated with an increased harvest index (HI) (Austin et al., 1980; Slafer and Andrade, 1991; Reynolds et al., 1999). However, above-ground biomass did not change (Slafer et al., 1990), or only slightly increased (Austin et al., 1980), or even decreased by 10% (Feil and Geisler, 1988).

The amount of nitrogen (N) present in the entire above-ground biomass changed little over the years. It varied mainly with the amount of above-ground biomass (Austin et al., 1977), N concentration itself appearing to play a minor role. The N harvest index (NHI) was greater for the newer than for the older cultivars in a fertile environment (Austin et al., 1980). The greatest NHI was 0.7 to 0.8, and it seems difficult to exceed this value because a minimum of energy is necessary for N uptake and N reduction. Ortiz-Monasterio et al. (1997) studied genetic progress in nitrogen use efficiency (NUE), defined by Moll et al. (1982) as grain yield per unit of available N. They grew 10 wheat cultivars released in Mexico from 1950 to 1985 with four N fertilization rates. Genetic gains in both grain yield and NUE were 30, 40, 60, and 90 kg ha^{-1} yr^{-1}, respectively, when N was provided at 0, 75, 150, and 300 kg ha^{-1}. This improved NUE resulted from either an improved uptake efficiency (plant N per unit of N taken up from the soil) or a greater N utilization efficiency (grain yield

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Abbreviations: G, genotype; HI, harvest index; KN, kernel number per square meter; L, location; N, nitrogen; NHI, nitrogen harvest index; NUE, nitrogen use efficiency; R, replication; TKW, 1000-kernel weight; T, treatment; and Y, year.

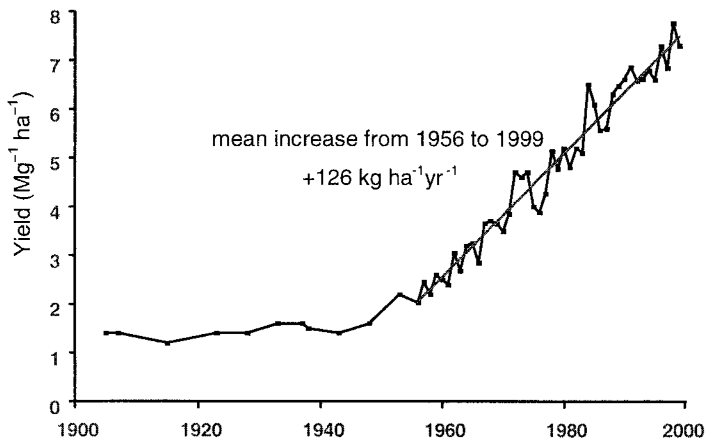

Fig. 1. Changes in wheat grain yield in France from 1900 to 2000.

per unit of N in the plant). The amount of N in the grain seems to be associated with a higher N uptake after anthesis during the grain-filling period (Cox et al., 1985).

The experiments described below were performed to assess the changes in agronomic traits of winter wheat cultivars bred and cultivated in France over the second half of the 20th century.

MATERIALS AND METHODS

Plant Material and Experimental Design

A group of 14 wheat cultivars released in France from 1946 to 1992 (Table 2) was studied. They commonly were grown in France during this period and covered 30 to 70% of the total area of cultivation. They were grown at five locations representative of the climate and soil in northern France: Mons (49°56′ N, 2°56′ E), Chartainvilliers (48°35′ N, 1°35′ E), Rennes (48°05′ N, 1°4′ W), Dijon (47°19′ N, 5°01′ E), and Clermont-Ferrand (45°47′ N, 3°5′ E). Field trials were conducted over 2 yr (1994–1995).

Four agronomic treatments were applied: combinations of two levels of fungicide (total foliar disease control or none) and two levels of N fertilizer. Low N level without fungicide represented the treatment applied by farmers in France several decades ago, while high N level with fungicide represented the more current practice. N fertilizer was applied at each location according to a predictive balance sheet method (Rémy and Hébert, 1977) with respective grain yield objectives of 6 Mg ha^{-1} (low N) and 9 Mg ha^{-1}(high N). In each location, mineral N in soil was measured in February from samples in the upper 120 cm soil profile. It varied among locations from 110 to 125 kg ha^{-1}. Low N objective was obtained without N fertilizer in all locations, the soils providing enough mineral N. N fertilizer supply varied among locations from 40 to 100 kg ha^{-1} at the higher N objective. It was applied in one rate at tillering when the N fertilizer supply was low (40 kg ha^{-1}) or

Table 1. Assessment of genetic gain in wheat yield: from a direct comparison of old and modern cultivars grown simultaneously (A) and from databases where common controls were used to estimate relative gains in yield (B).

A.

Country	Period	Number of genotypes	Gain† (kg ha^{-1} yr^{-1})	Reference
France	1918–1938	5	39.0	Jonard and Koller, 1951
France	1925–1978	10	50.0	Masle, 1985
UK	1908–1978	12	30.0	Austin et al., 1980
UK	1908–1985	13	38.0	Austin et al., 1989
Sweden	1900–1970	20	12.6	Ledent and Stoy, 1988
Germany	1921–1978	10	15.8	Karpenstein-Machan and Scheffer, 1989
			12.8	
Western Australia	1884–1982	27	5.8	Perry and d'Antuono, 1989
Mexico (N–W)	1950–1982	14	59.0	Waddington et al., 1986
USA (Kansas)	1919–1987	38	16.0	Cox et al., 1988
USA (North Dakota)	1911–1979		14.0	Deckerd et al., 1985

B.

Country	Period	Genetic gain/national gain (%)	National gain‡	Reference
UK	1947–1975	50	80%	Silvey, 1978
UK	1947–1978	63	105%	Silvey, 1981
UK	1947–1983	45	167%	Silvey, 1986
France	1957–1980	33	120 kg ha^{-1} yr^{-1}	Guyonnet, 1980
France	1880–1930	–	25 kg ha^{-1} yr^{-1}	Moule, 1994
France	1930–1950	–	37 kg ha^{-1} yr^{-1}	Moule, 1994
France	1880–1950	–	28 kg ha^{-1} yr^{-1}	Moule, 1994
Hungary	1961–1983	46	135 kg ha^{-1} yr^{-1}	Balla et al., 1986
Germany	1952–1981	38	–	Schuster et al., 1982

† Yield of dry grain at 0 g kg^{-1} moisture content.
‡ National yield increase during the period under study.

Table 2. Some agronomic and other characteristics of the 14 winter wheat cultivars investigated in this report.

Cultivar	Code	Year of registration	Earliness†	Height (cm)	Response to gibberellic acid		Yield low N without fungicide (Mg ha^{-1})	Yield high N without fungicide (Mg ha^{-1})	Yield low N with fungicide (Mg ha^{-1})	Yield high N with fungicide (Mg ha^{-1})	Ratio of optimum yield to mean yield in France§
Cappelle	CPL	1946	152	118	s‡	–	5.9	5.8	6.5	6.6	4.4
Étoile de Choisy	EDC	1950	136	116	s	–	5.5	5.7	6.3	6.7	3.5
Champlein	CHA	1959	148	115	s	–	6.1	5.9	7.0	7.2	2.8
Capitole	CPI	1964	142	104	s	–	6.2	6.1	7.1	7.8	2.6
Talent	TAL	1973	139	96	s	–	6.4	6.6	7.5	8.2	1.8
Courtot	COU	1974	141	78	i	Rht1 + Rht2	5.5	6.3	6.9	8.3	1.9
Arminda	ARM	1977	151	105	s	–	6.9	7.7	7.7	8.7	2.0
Fidel	FID	1978	143	109	s	–	6.4	6.2	7.3	7.8	1.7
Thésée	THE	1983	142	96	s	–	6.4	6.7	8.0	9.4	1.7
Pernel	PER	1983	147	92	i	*Rht2* + ?	7.2	7.6	8.2	9.2	1.7
Soissons	SOI	1987	139	92	i	Rht1	6.9	7.3	8.4	9.4	1.6
Renan	REN	1989	145	102	i	Rht1	6.8	7.8	7.2	8.3	1.6
Arche	ARC	1989	145	99	s	–	7.5	7.9	8.8	9.5	1.5
Alliage	ALL	1992	146	96	i	Rht2	7.5	8.6	8.2	9.3	1.4
						mean	6.5	6.9	7.5	8.3	

† Heading date, in days from 1 January.
‡ i: GA insensitive (dwarfing gene *Rht1* or/and *Rht2*); s: GA sensitive.
§ Ratio of the yield of the variety in the trial with high N and fungicide to the mean yield of wheat in France when the variety was registered.

in two rates—at tillering and stem elongation—when the N fertilizer supply was higher (60–100 kg ha^{-1}).

The two treatments without fungicide were lacking at Clermont-Ferrand in 1994. Adverse growing conditions were encountered at Rennes in 1995, where the plots were infected with the take-all fungus [*Gaeumannomyces graminis* (Sacc.) Arx & D. Olivier var. *tritici*], which was not controlled by the fungicide used. At Chartainvilliers, lodging occurred in 1994 and 1995, and deficient seed was set in 1995. The multilocation analysis achieved a greater accuracy for most variables by discarding Chartainvilliers in 1994 and 1995 and Rennes in 1995. A total of 26 location × year × treatment combinations were thus available.

The four treatments were applied in a randomized complete block design with three replications. The main plot consisted of three adjacent subplots to minimize edge effects. Subplot size varied from 5 to 6.5 m^2 according to the location. The whole central subplot was harvested.

Plant Sampling and Observations

From each center subplot at maturity, 160 tillers were sampled to assess total dry matter and yield components. The sample consisted of 20 tillers randomly sampled at eight spots within the plot. Strips (50 cm wide) from each end of the plot were removed to eliminate border effects. The remaining plants in the center of the plot were harvested with a combine. The amount of grain in the sample was added to that from the mechanically harvested area. Date of heading, when 50% of the tillers had reached spike emergence, lodging, and disease sensitivities also were recorded. The amount of N in the straw and grain was determined by a Kjeldahl procedure (Jackson, 1958; X31-111 AFNOR standard, 1987) from subsamples of the straw and grain from the 160 tillers. In 1994, these values were collected for each of the four treatments from Chartainvilliers, Clermont-Ferrand and Mons on only two cultivars: Soissons, which was the highest yielding cultivar, and Cappelle, which was the poorest. N data on all treatment × cultivar combinations were available for Dijon and Rennes in 1994, and from all sites in 1995.

The mechanically harvested grain was weighed and a sample of grain was dried in an oven at 105°C for 24 h to determine grain moisture content. Each sample of 160 tillers was also dried.

Variables and Statistical Analysis

TKW was assessed by counting the number of kernels contained in 100 g. The yield components were determined from the samples according to the following adjustment:

$$\text{Component m}^{-2} = \frac{\text{Sample value} \times \text{Grain yield m}^{-2}}{\text{Sample grain weight}}$$

The other variables estimated were total above-ground dry weight at maturity, vegetative biomass, and HI as a percentage of grain in the entire above-ground biomass. KN values were estimated by dividing the grain yield by the TKW and adjusting for area. The number of kernels per spike, the number of kernels per vegetative biomass and the chaff dry matter weight, as an estimate of the size of the spike, were estimated from the sample of 160 tillers. The amount of protein was estimated from the amount of N multiplied by a factor of 5.7 (nitrogen AACC method, 1990). Nitrogen uptake corresponded to the total amounts of nitrogen accumulated in the grain and in the straw + chaff. The NHI was obtained by dividing the amount of N in the grain at maturity by that in the entire above-ground biomass.

The year of varietal release was considered to be a continuous quantitative variable and was used as a regressor in the linear regression analysis to calculate the genetic gains for each agronomic trait. R^2 is defined as the ratio between the sum of squares explained by the linear regression and the total sum of squares. The agronomic traits of each cultivar were assessed separately for each of the four treatments and across treatments. The release dates of the 14 cultivars defined two time periods: a phase before 1973 without semidwarf cultivars and a period of subsequent semi-dwarf wheat improvement. The contribution of the dwarfing genes was noted with lines of the second period including the four semidwarf cultivars (Alliage, Pernel, Renan, Soissons) and four cultivars of conventional stature (Arche, Arminda, Fidel, and Thésée).

The response of each cultivar to the fertility conditions of the location were estimated by the joint regression model (Finlay and Wilkinson, 1963). Analysis of variance and regressions were performed with SAS Institute Inc. (1989). Joint regression analysis and the corresponding plot depiction were performed with the INTERA package on a PC (Decoux and Denis, 1991). Effects were evaluated according to the following analysis of variance model:

Table 3. Mean, range, root mean square error (MSE) and coefficient of variation of grain yield and yield components.

Variable	Unit	Mean	Minimum	Maximum	Root MSE	CV (%)
Grain yield	Mg ha^{-1}	7.4	3.3	11.9	0.4	4.9
Above-ground biomass	kg ha^{-1}	15 849	9 579	25 616	954	6.0
Straw yield	kg ha^{-1}	9 415	5 250	18 478	749	8.0
Harvest index		41.3	16.1	63.0	1.7	4.2
Kernel number/m^2		17 094	8 951	27 429	1 070	6.3
1000-Kernel weight	g	38.9	22.2	52.7	1.7	4.4
Spike number/m^2		514	239	981	41	7.9
Kernel number/spike		33.9	16.5	57.3	2.1	6.2
Chaff	kg ha^{-1}	3 629	1 280	8 687	391	10.8
Kernel number/gram of straw		18.5	5.8	30.5	1.2	6.6

$$Y_{gyltr} = \mu + G_g + Y_y + L_l + T_t + R_{y/r} + (G \times Y)_{gy} + (G \times L)_{gl} + (G \times T)_{gt} + (Y \times L)_{yl} + (Y \times T)_{yt} + (L \times T)_{lt} + (G \times Y \times L)_{gyl} + (G \times Y \times T)_{gyt} + (G \times L \times T)_{glt} + (Y \times L \times T)_{ylt} + (G \times Y \times L \times T)_{gylt} + \varepsilon_{gyltr}$$

where Y_{gyltr} is a given observation for genotype g grown in year y in location l with agronomic treatment t in replication r, μ is the grand mean, G_g is the genotype main effect, Y_y is the year main effect, L_l the location main effect, T_t is the treatment main effect, $R_{y/r}$ is the effect of replication r in year y and location l, and the last term ε_{gyltr} is the residual. All other terms describe interactions.

RESULTS AND DISCUSSION

Genetic Improvement in Wheat Grain Yield

Mean grain yield reached 7.4 Mg ha^{-1} on average. Multilocation analysis revealed good accuracy, with a coefficient of variation of 4.9% (Table 3). This high yield was only partly due to the cultivar improvement, since the genotype mean square was smaller than the treatment mean square (Table 4). The improvement was also a consequence of different interactions, the most important being the interactions with treatment (Table 4). Although N fertilizers were applied to achieve grain yield objectives of 6 Mg ha^{-1} (low fertility) and 9 Mg ha^{-1} (high fertility), the final mean difference between the two fertility levels was less than 1 Mg ha^{-1}. However, the low nitrogen treatment without fungicide reached 6.5 Mg ha^{-1} and the high nitrogen treatment with fungicide 8.3 Mg ha^{-1} (Table 5). Considering the best value obtained per location, the objective of 9 Mg ha^{-1} was indeed exceeded for some genotypes (Table 5).

Table 4. Analysis of variance for grain yield.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F	P
Genotype (G)	13	642.4	49.41	380.5	*
Year (Y)	1	9.3	9.28	71.5	*
Location (L)	3	141.5	47.15	363.1	*
Treatment (T)	3	462.5	154.17	1187.2	*
Replication	54	43.8	0.81	6.3	*
G × Y	13	34.9	2.68	20.7	*
G × L	39	72.9	1.87	14.4	*
G × T	39	121.2	3.11	23.9	*
Y × L	2	0.9	0.46	3.6	*
Y × T	3	35.8	11.95	92.0	*
L × T	9	249.1	27.68	213.2	*
G × Y × L	26	21.4	0.82	6.3	*
G × Y × T	39	16.5	0.42	3.3	*
G × L × T	117	86.4	0.74	5.7	*
Y × L × T	4	27.5	6.87	52.9	*
G × Y × L × T	52	14.1	0.27	2.1	*
residual	702	91.2	0.13		

* Significant at the 0.05 probability level

Genetic gains were estimated by several means per cultivar (Table 5): the grand mean, means per group of treatments (treatments with high/low nitrogen inputs or treatments with/without fungicide), and means per treatment. They also were assessed by the mean of optimal practices per location or the best yield resulting from one location × year × treatment combination for a given cultivar.

The mean genetic gain for grain yield was estimated from the mean of all agricultural practices and reached 49 kg ha^{-1} yr^{-1} (Table 5). In all cases, genetic gain exceeded zero at the 0.05 probability level. It varied from 36 kg ha^{-1} yr^{-1} at the low level of N input without fungicide, to 63 kg ha^{-1} yr^{-1} at the high level of N input with fungicide. This range was even greater when considering the 26 location × year × treatment combinations, as genetic gain tended to increase slightly with the average yield of the trial. This suggests that modern cultivars are better adapted to high input agriculture. N supply provided a further increase of 20 kg ha^{-1} yr^{-1} while fungicides gave an additional increase of 7 kg ha^{-1} yr^{-1} (Table 5). There was an interaction between nitrogen and fungicide supplies, which was partly due to severe leaf rust on some modern cultivars in some locations. This occurred for two high yielding cultivars, Soissons and Thésée, which were highly susceptible to leaf rust.

For each location × year pair, the optimal N fertilization treatment differed between cultivars. Old cultivars obtained their best yields with low N input, while modern cultivars were best at the higher input level. When the genetic gain was assessed with the highest yield obtained by the cultivars at a given treatment in each location, genetic gain reached 57.1 kg ha^{-1} yr^{-1} (Table 5). Some cultivars were possibly negatively affected by high N inputs, as the average yield calculated from the highest achieved yields was better than that resulting from just basing it on the high input treatments (Table 5).

These assessments are in agreement with those found elsewhere in Europe (Austin et al., 1980; Austin and Ford, 1989; Balla et al., 1986) or in Mexico (Waddington et al., 1986). Analysis of published data seems to show that genetic gain accelerated during the second half of the 20th century.

Our study, and those of Jonard and Koller (1951) and Masle (1985), show that grain yield potential was at

Table 5. Genetic gain per year for grain yield, biomass, harvest index calculated at diverse levels of fertility by linear regression of the average yield on the year of registration of cultivars.

	Grain yield			Total above-ground biomass			Vegetative above-ground biomass			Harvest index		
Agricultural practice	Mean ($Mg\ ha^{-1}$)	Gain ($kg\ ha^{-1}\ yr^{-1}$)	R^2	Mean ($kg\ ha^{-1}$)	Gain ($kg\ ha^{-1}\ yr^{-1}$)	R^2	Mean ($kg\ ha^{-1}$)	Gain ($kg\ ha^{-1}\ yr^{-1}$)	R^2	Mean (%)	Gain (% yr^{-1})	R^2
Grand mean	7.4	49.0*	0.83	15 846	ns	ns	9 414	ns	ns	41.3	0.20*	0.63
Nitrogen adjusted for 6 Mg/ha	7.1	38.9*	0.71	14 848	ns	ns	8 702	ns	ns	42.1	0.19*	0.63
Nitrogen adjusted for 9 Mg/ha	7.7	59.1*	0.87	16 842	ns	ns	10 126	ns	ns	40.4	0.22*	0.63
Without fungicide	6.7	45.1*	0.72	15 187	ns	ns	9 280	ns	ns	39.0	0.20*	0.67
With fungicide	7.9	52.3*	0.81	16 384	ns	ns	9 524	ns	ns	43.1	0.21*	0.59
Low nitrogen without fungicide	6.5	35.7*	0.63	14 282	ns	ns	8 530	ns	ns	40.4	0.19*	0.70
High nitrogen without fungicide	6.9	54.4*	0.73	16 095	ns	ns	10 034	ns	ns	37.6	0.20*	0.60
Low nitrogen with fungicide	7.5	41.6*	0.70	15 313	ns	ns	8 843	ns	ns	43.6	0.19*	0.56
High nitrogen with fungicide	8.3	62.9*	0.84	17 447	ns	ns	10 202	ns	ns	42.6	0.24*	0.61
Best value obtained per location	8.7	57.1*	0.54	18 585	36.9*	0.12	11 381	ns	ns	46.6	0.20*	0.24
Best value	9.6	66.0*	0.77	19 624	ns	ns	12 506	−57.4*	0.29	52.8	0.21*	0.35

* Significant at the 0.05 probability level.

least 6 Mg ha^{-1} in France 50 yr ago, i.e., four times higher than the national yield at that time. Similar yields were obtained by Ledent and Stoy (1988) for Sweden, and by Austin et al. (1980) in the UK. In 1992, this ratio of potential to national yield fell to 1.4 in France (Table 2). Much of the genetic gain can probably be attributed to the adaptation of the cultivars to new agricultural practices. It also can be expected that the gap between yield potential and national yield will further be reduced in the coming years if average national yields continue in the same trend. The evaluation of cultivar improvement also depends on the cultivars sampled. The first half period of our study was represented by four cultivars that covered more than 75% of the wheat area grown in France for 20 yr, while the second half period was represented by 10 genotypes of smaller areas.

The slopes of joint regression models (Finlay and Wilkinson, 1963) can help to assess the ability to exploit the fertility of the environment. The grain yield of each cultivar in each of the 26 environments (combinations of year × location × treatment) was regressed against the mean of all 14 cultivars in those same environments. The slopes ranged from 0.65 for Cappelle to 1.46 for Thésée (Fig. 2). Most of the modern cultivars, with the exception of Alliage and Renan, had higher slopes than old cultivars. A wheat cultivar with a low slope and a grain yield as high as the best cultivars cultivated at high input agriculture could be defined as a "hardy" wheat, a high-yielding stable cultivar. Alliage and Renan are more stable and high yielding than the old cultivar Cappelle. Thésée and Soissons behaved well in favorable environments but their yield decreased when yield-limiting factors occurred, making them less stable. Selection has long created cultivars more adapted and responsive to increased amounts of inputs than their predecessors. Thus it is possible to find modern cultivars that outyield old cultivars, even in low input agriculture, as it is shown in the present study.

Grignac et al. (1981) made similar conclusions in a comparison of four modern cultivars (Etoile de Choisy, Capitole, Talent, and Courtot) to four old cultivars bred from local populations of the early 20th century (Bladette de Besplas, Saisette d'Arles, Poilu du Tarn, and Touzelle blanche de Provence). These eight cultivars were grown in the mediterranean region of France from 1974 to 1980 in pure lines or in mixtures at two levels of input. In 1974, the mixture used contained 12.5% each of the eight cultivars. This proportion slightly varied during the following years according to the level of inputs. In the mixtures, the proportion of plants was the

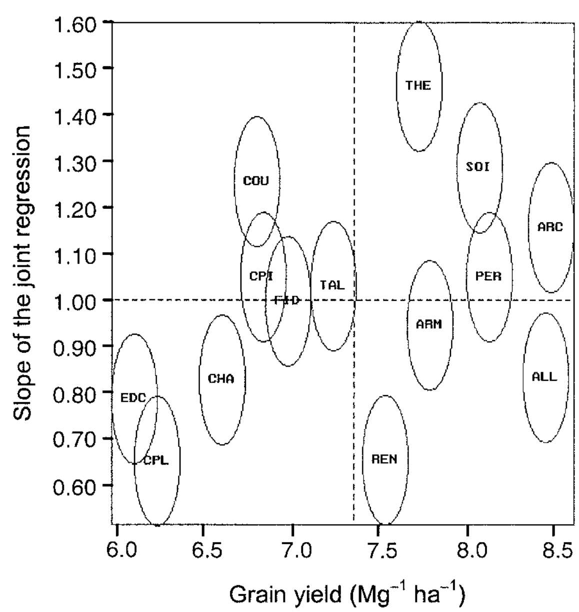

Fig. 2. Slopes of joint regression and main grain yield for the cultivars. The slope estimates the cultivar response to the fertility of each environment. Indication of the variability of the estimates is given by the ellipses at the 0.05 probability level. Mean grain yield is symbolized with a vertical dashed line. The horizontal line separates genotypes specifically adapted to favorable environments (slope > 1) and genotypes specifically adapted to unfavorable environments (slope < 1). Codes of the cultivars are the same as in Table 2.

Table 6. Genetic gain per year for some yield components calculated at diverse levels of fertility by linear regression of the average yield on the year of registration of cultivars (1000-kernel weight not given because not significant).

	Number of kernels/m^2			Chaff dry matter/spike			Number of kernels/gram of straw		
Agricultural practice	Mean	Gain (yr^{-1})	R^2	Mean (kg ha^{-1})	Gain (kg ha^{-1} yr^{-1})	R^2	Mean	Gain (yr^{-1})	R^2
Grand mean	17 096	115*	0.47	3 631	27.7*	0.46	18.6	0.15*	0.48
Nitrogen adjusted for 6 Mg/ha	15 722	96*	0.41	3 957	29.2*	0.46	18.4	0.14*	0.51
Nitrogen adjusted for 9 Mg/ha	18 476	134*	0.50	3 303	26.1*	0.45	18.7	0.15*	0.45
Without fungicide	16 720	116*	0.46	3 546	25.1*	0.41	18.4	0.15*	0.47
With fungicide	17 399	115*	0.47	3 700	29.9*	0.48	18.7	0.15*	0.47
Low nitrogen without fungicide	15 309	96*	0.42	3 926	25.9*	0.39	18.3	0.15*	0.56
High nitrogen without fungicide	18 148	137*	0.47	3 160	23.9*	0.43	18.5	0.14*	0.39
Low nitrogen with fungicide	16 054	96*	0.39	3 983	31.8*	0.50	18.5	0.13*	0.45
High nitrogen with fungicide	18 743	133*	0.52	3 417	27.9*	0.45	18.9	0.16*	0.48
Best value obtained per location	19 962	129*	0.35	4 584	29.6*	0.08	21.5	0.15*	0.30
Best value	21 854	121*	0.41	6 408	35.6*	0.30	24.1	0.16*	0.46

* Significant at the 0.05 probability level.

same for the old and modern cultivars at low input agriculture, excepting the short variety Courtot. But the proportion of modern cultivars, with the exception of Courtot, increased at the higher input level. This indicated that modern cultivars expressed a higher responsiveness to improved conditions and an equal to higher ability for competition than the older cultivars.

Contribution of Biomass, Harvest Index and Yield Components to the Genetic Improvement in Wheat Grain Yield

The improvement in grain yield was associated with an increase in the HI of 0.2% per year (Table 5) and with an increase in KN of 115 kernels m^{-2} yr^{-1} (Table 6). Recent lines were better able to produce more kernels from the vegetative biomass than the old lines. The number of kernels per unit of vegetative biomass almost doubled from 12.9 (Cappelle) to 22.2 (Alliage) kernels g^{-1} and corresponded to an increase of 0.15 kernels g^{-1} yr^{-1} (Table 6). However, these means were associated with great variations among cultivars released at a same period. For instance, HI varied from 41 to 46% and KN varied from 15,000 to 21,000 for cultivars introduced between 1989 and 1992 (data not shown). Higher HI was mainly related to the reduction of height ($r = -0.65$, significant at the 0.05 probability level). Yield increase also has been related to KN and HI in many studies as reported by Slafer and Andrade (1991) and Reynolds et al. (1999). The biomass production was similar among the two groups, modern cultivars and old cultivars (Table 5). This behavior seemed to be a common trend reported in the literature (Slafer and Andrade, 1991; Reynolds et al., 1999).

We found no relationship between the genetic gain for grain yield and the TKW; TKW changed little over the years (Table 6). This would indicate that the total amount of available assimilates in the experiment was large enough for growing the numerous kernels of the modern cultivars. These results differed from those reported in the literature (Slafer and Andrade, 1991) where the gains in KN were partially compensated by reductions in individual kernel weight. Slafer and Miralles (1993) compared three cultivars released at different times in Argentina (1920, 1940, and 1980) and showed that the modern cultivar had lower TKW than the old cultivars when considering the average of all kernels, but the basal kernels of its central spikelets were as heavy as those of the two other cultivars. The authors suggested that the additional kernels should be placed in distal positions within the central spikelets and that these additional kernels would not compete for current assimilates with the basal ones. This was supported by another study of Slafer and Miralles (1992) performed on another wheat cultivar released in Argentina in 1980. The authors showed that the TKW was increased when spikes were cut in half, doubling the source–sink ratio. The physiological potential for increasing kernel weight at distal spikelet positions can be expected to be as much as 16% (Reynolds et al., 1999).

The increase in KN was due to the size and fertility of the spike. The chaff dry matter per spike, as an estimate of the size of the spike, increased by 28 kg ha^{-1} yr^{-1} on average from 1946 to 1992 (Table 6). But the cultivars differed in how the high KN values were achieved. Talent could produce many small spikes, more than the oldest cultivars, while Renan and Thésée produce fewer but heavier spikes. Soissons was intermediate in most values. Modern cultivars generally produced more kernels from the vegetative biomass available than the old cultivars.

It seemed likely that improvements achieved by breeding new cultivars have mainly resulted in a greater ability to fill an increasing number of kernels. TKW is maintained for a higher KN in modern cultivars than in older cultivars (data not shown). Thus the relationship between TKW and KN has improved.

Contribution of Nitrogen Components to the Genetic Improvement in Wheat Grain Yield

The NHI, estimated by the amount of N in the grain divided by that in the total above-ground biomass, was greater for the newer cultivars than for the older ones. This percentage increased by 0.15% yr^{-1} starting from 1946 (Table 7). The older cultivars Etoile de Choisy and Cappelle recorded 67% on average, while this value increased to 70 to 75% for the cultivars introduced after 1980. The increase in the NHI was correlated with that of the HI (r = 0.75, significant at the 0.05 probability

Table 7. Genetic gain per year for nitrogen characteristics calculated at diverse levels of fertility by linear regression of the average yield on the year of registration of cultivars.

	Grain protein			Nitrogen harvest index			N absorbed per 1000 kernels		
Agricultural practice	Mean (%)	Gain (% yr^{-1})	R^2	Mean (%)	Gain (% yr^{-1})	R^2	Mean (g)	Gain (g yr^{-1})	R^2
Grand mean	11.6	−0.040*	0.55	70.3	0.15*	0.57	1.40	−0.0086*	0.39
Nitrogen adjusted for 6 Mg/ha	11.3	−0.038*	0.53	73.2	0.13*	0.69	1.37	−0.0081*	0.41
Nitrogen adjusted for 9 Mg/ha	11.9	−0.043*	0.54	67.4	0.17*	0.48	1.43	−0.0090*	0.36
Without fungicide	11.6	−0.036*	0.50	67.4	0.15*	0.44	1.37	−0.0078*	0.36
With fungicide	11.6	−0.044*	0.56	73.1	0.16*	0.58	1.43	−0.0093*	0.40
Low nitrogen without fungicide	11.3	−0.033*	0.44	71.3	0.14*	0.58	1.34	−0.0073*	0.37
High nitrogen without fungicide	11.8	−0.040*	0.53	63.6	0.15*	0.32	1.39	−0.0082*	0.33
Low nitrogen with fungicide	11.3	−0.043*	0.56	75.1	0.13*	0.64	1.40	−0.0089*	0.43
High nitrogen with fungicide	11.9	−0.045*	0.52	71.2	0.19*	0.50	1.47	−0.0097*	0.35
Best value obtained per location	13.1	−0.045*	0.27	79.0	0.08*	0.09	1.70	−0.0151*	0.23
Best value	14.2	−0.034*	0.19	82.7	0.07*	0.16	2.15	−0.0236*	0.48

* Significant at the 0.05 probability level

level). The NHI depended on the treatment while the grain protein percentage changed little between the treatments (Table 7): nitrogen gave a further increase of 0.4% while fungicide gave an increase of 0.1%. There was considerable variation in the NHI at different environments: from 37 to 81 for Etoile de Choisy and from 61 to 86 for Arminda (individual data not shown). The difference between the cultivars decreased as the yield potential for the environment increased. In contrast, Austin et al. (1980) found that the NHI was greater for the newer than for the older cultivars in low fertility conditions, but not in high fertility situations. Newer cultivars generally had lower N concentrations in the grain than the older ones (Table 7), but had a greater total N yield per unit area. The decrease in N concentration was due to dilution. The N concentration also was influenced more by treatment than by cultivar.

Effect of Dwarfing Genes on Grain Yield and Yield Components

For all variables, genetic gains were not significant within groups of cultivars (group of semi-dwarf cultivars and group of conventional ones) since the number of genotypes was too small. However, differences in grain yield and yield components between the two groups were quite important. For the cultivars registered since 1980 (Table 8), cultivars containing dwarfing genes (*Rht*1 or *Rht*2) significantly outyielded the others on average by 0.3 Mg ha^{-1}. As there was no difference in lodging sensitivity between these two groups, this suggests that the dwarfing genes directly affect grain yield. This effect was somewhat more pronounced at the high input levels. In the UK, Gale and Youssefian (1985) also reported that *Rht* genes helped accelerate the increase in grain yield after 1975.

Dwarfing genes only had a small significant effect on biomass production, as semidwarf lines yielded 2% less than the taller lines (Table 8). In the case of vegetative biomass, they produced 6% less than the taller cultivars. Contrary to the common belief, reducing plant height did not severely reduce vegetative biomass.

KN and KN per spike were similar between the two groups, while TKW was higher for semidwarf lines. Semi-dwarf lines were better able to fill a similar number of kernels than the conventional lines, since they produced more chaff and more kernels per gram of vegetative biomass, respectively, 4225 and 3814 kg ha^{-1}; 20.3 and 18.9 kernels g^{-1} (Table 8).

CONCLUSIONS

Our results show that varietal improvement played a major role in the increase in winter wheat yield after 1946 in France. Its contribution to the increase in the national yield depended on the agricultural practices used, and varied from one third to one half. Genotype × environment interactions contributed partly to that gain as modern cultivars were more suitable and responsive for increased inputs than were their predecessors. As argued by Austin (1999), a change in any component of the environment may provide opportunities to breeders to modify their wheat genotypes to better exploit the new environment. The first causal factor for the gain in yield was the reduction of plant height. The new cultivars have shorter straw, resulting in a higher HI. They have more consistent yields because they are less susceptible to lodging, allowing a better use of N. Although most of modern cultivars possess one dwarfing gene, some conventional cultivars without dwarfing genes are as short as semidwarf cultivars. The reduction in height during the second half of the 20th century was not associated with a decrease in biomass production. The second

Table 8. Effect of dwarfing genes on grain yield and yield components for the cultivars released since 1977.

Rht gene	Grain yield	Above-ground biomass	Vegetative biomass (kg ha^{-1})	Harvest index	Kernel number	1000-Kernel weight	Spike number	Kernel number/spike	Chaff	Kernel number/ gram of straw	Height
	Mg ha^{-1}	kg ha^{-1}			m^{-2}	g	m^{-2}		kg ha^{-1}		cm
One	8.1 a†	16 200 b	9 193 b	44.1 a	18 340 a	39.6 a	491 b	37.6 a	4 225 a	20.3 a	95 b
None	7.8 b	16 558 a	9 786 a	41.5 b	18 249 a	38.2 b	497 a	37.5 a	3 814 b	18.9 b	102 a

† Means followed by a common letter within a column were not significantly different at the 0.05 probability level, according to Student-Newman-Keuls test.

factor of improvement is a greater ability to produce more kernels from a given biomass production. This produced a great increase in the number of kernels per unit area. Breeding created cultivars that were able to fill these additional kernels. The negative relationship between the TKW and KN was therefore shifted.

Modern cultivars used N more efficiently than the older ones. A wheat cultivar that produces grain yields under low inputs similar to those of the best cultivars cultivated at high input levels is considered to be a "hardy" wheat, a stable high-yielding cultivar. Recent cultivars are generally more stable and high-yielding than the older ones, despite the commonly held belief to the contrary. This result is promising in a context where agricultural practices in Europe are likely to go toward more extensive systems with lower inputs. It indicates that it is possible to develop cultivars adapted to both low and high fertility conditions.

It is difficult to predict the improvement of yield in the future. A further increase in the total biomass may be achievable as modern cultivars still vary for it. In 1980, Austin calculated that breeders may be able to increase HI up to 60%. As our results were lower, breeding for such a high HI without reducing vegetative biomass and for an increasing ability to produce more kernels from the vegetative biomass may be still achievable.

The future challenge will be to obtain the same genetic gains in low-input systems as in high-input systems.

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