

Grain yield, nitrogen-use efficiency and baking quality of old and modern Italian bread-wheat cultivars grown at different nitrogen levels

Giovanni Guarda^a, Silvano Padovan^a, Giovanni Delogu^{b,*}

^a *Institute of Genetics and Agricultural Research “N. Strampelli”, Administration of the Province of Vicenza,
Via Marconi 1, 36645 Lonigo (VI), Italy*

^b *Experimental Institute for Cereal Research, Via S. Protaso 302, I-29017 Fiorenzuola d’Arda (PC), Italy*

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Abstract

The high yields of today’s modern wheat cultivars require high input which leads to both higher production costs and a greater risk of environmental pollution. Increasing public awareness of the latter, along with growing consumer demand for healthier products, has led on one hand to greater criticism being leveled at this type of production model and on the other to heightened emphasis on crops grown under integrated-management and organic systems. This applies also to wheat. By contrast, the yield increments registered by the new wheat cultivars during this period have been bolstered by the progressively higher N-inputs. All that has led to the idea that modern cultivars selected under conditions of high N-input are little suited to low-input conditions with respect to old wheat populations and cultivars. The present study investigated the responses of grain yield and quality and N-use efficiency at three input rates (N_0 , N_{80} , N_{160} , kg ha⁻¹) in a set of 16 of the most representative bread-wheat cultivars from 1900 to 1994.

The average yield rise throughout the time was 33.5 kg ha⁻¹ per year, due to an increase of 124 kernel number per square meter per year and of 0.22% per year for harvest index (HI). At the same time, grain N-accumulation increased from 0.21 kg ha⁻¹ per year at N_0 rate to 0.67 and 0.82 kg ha⁻¹ per year for N_{80} and N_{160} , respectively. This increase was matched by average yield increments of 44, 50 and 47 kg per kg of N-accumulated. The cultivars exhibited a progressive rise in demand for N-supply over time of release so as to maximize yields accompanied by the upgraded capacity of N-use and enhanced quality traits: alveograph’s *W*-index and *P/L* dough-gluten index rose from values between 65–170 and 0.25–0.39 for cultivars from 1900 to 1970 to 174–241 and 0.48–0.52 for those released after 1970. All the data show that over the last century the target of upgrading both yield amounts and grain quality for bread-making was successfully achieved. This success also indirectly led to an improved plant nitrogen uptake and use, clearly indicates that even under conditions of limited inputs or under organic-farming practices the best results are to be achieved by employing not old populations or varieties but modern cultivars, the latter being the only ones with the intrinsic traits capable of ensuring yield and quality at low N-supply even though they maximize their traits at high nitrogen inputs.

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* Corresponding author. Tel.: +39-0523-983758; fax: +39-0523-983750.

E-mail address: g.delogu@iol.it (G. Delogu).

1. Introduction

The high yields of today's modern wheat cultivars require the use of mineral fertilizers and chemical herbicides and fungicides, all of which lead to both higher production costs and a greater risk of environmental pollution. Increasing public awareness of this, along with growing consumer demand for healthier products, has led on one hand to greater criticism of this type of production and on the other to a greater emphasis on crops grown under integrated-management and organic systems. The organic approach, which largely reprises the techniques in use before the introduction of mineral fertilizers and chemical weed and disease control treatments, appears to be based on the assumption that a return to such farming methods can ensure products that are both healthier and of higher quality than the standard production grown under today's intensive and integrated agriculture systems.

This applies also to wheat, and one school of thought views the old populations and cultivars grown in the early 20th century as being the best suited to low-input and organic growing systems because they are presumably endowed with greater adaptability and 'hardiness' as a result of a greater tolerance to diseases and a more efficient capacity for using nitrogen (N) in the soil (Grignac et al., 1981). Soil N is a particularly important issue as it plays a key role in achieving quantitatively and qualitatively high yields, although its easy leaching from the soil can result in the polluting of water tables. Indeed, it has been estimated that on average only 40–60% of mineral N-dressing for wheat is taken up by the crop and that percentage decreases as the N-input increases, resulting in higher residual soil N-amounts that can readily be leached (Ortiz-Monasterio et al., 1997; Foulkes et al., 1998; Austin, 1999; Raun and Gordon, 1999; Derici and Schepers, 2001).

Yet this school of thought does not appear to take into account the rise in yields due to the manipulations of the morphological, physiological and biochemical traits of the species and the introduction of resistance to pathogens and of tolerance to abiotic stresses as a result of advances in crop breeding and management practices, e.g. increasing optimization of N-inputs, phytosanitary protection and mechanization (Austin et al., 1980; Canevara et al., 1994; Calderini

et al., 1999). Grain yield per unit has risen over the last century by 110 kg ha^{-1} per year, essentially due to reduced plant height and fine-tuning among its various components, with the harvest index (HI) showing an average increase from 0.34 to 0.51 (Austin et al., 1989; Austin, 1999). The yield increments registered by the new wheat cultivars over this time, however, have been bolstered by progressively higher N-inputs (Austin, 1999) made possible by the greater tolerance to lodging of the new cultivars compared with the old ones. All this has led to the idea that the modern cultivars selected under conditions of high N-input are little suited to low-input conditions with respect to the old wheat populations and cultivars. While this assumption is supported in part by the finding that modern cultivars usually show lower grain protein concentration, there are many studies indicating improved N-use efficiency in modern cultivars (Calderini et al., 1995; Ortiz-Monasterio et al., 1997; Foulkes et al., 1998; Reynolds et al., 1999). Therefore, the present study investigated the responses of grain yield and quality and N-use efficiency at three varying input rates in a set of 16 of the most representative bread-wheat cultivars from 1900 to 1994.

2. Materials and methods

The trials were run at Lonigo in the Po valley in northern Italy (45.5°N 11.5°E , 36 m a.s.l.) from 1993 to 1996 on 16 Italian winter wheat cultivars: 2 populations grown in the early 1900s and 14 cultivars representative of the breeding activity conducted in the country from 1916 to 1994 (Table 1). The varieties were cultivated under N-input regimes of 0,80 and 160 kg ha^{-1} in a split-plot design with four replications. The main plots were the N-rates and the 10 m^2 sub-plots the cultivars. Each year the plots were rotated with silage maize. The soil was a clay-loam with pH 7.8 and a 2.1% average organic matter concentration. The sowing was in late October at 400 seeds m^{-2} . The pre-sowing inputs included 96 kg ha^{-1} of P, 96 kg ha^{-1} of K and 20% N in the N_{80} and N_{160} treatments. The remaining 80% N was applied as cover dressing in equal amounts on two dates: at three–four leaf stage and at the end of tillering. A weed control treatment was applied in the first 10 days of March using Ioxinil

Table 1

Cultivars selected in Italy in different periods during of the last century and their quality score

Cultivar	Year of introduction	Pedigree	Quality score ^a
Cologna Veneta	1900	Local population	8
Gentil Rosso	1900	Local population	7
Ardito	1916	Rieti/Wilhelmina//Akakomugi	9
Villa Glori	1918	Rieti/Wilhelmina//Akakomugi	6
Autonomia B	1930	Frassineto 405/Mentana	9
San Pastore	1940	Balilla/Villa Glori	6
Mara	1947	Autonomia/Aquila	6
Abbondanza	1950	Autonomia/Fontarronco	9
Gallini	1956	San Pastore/Carme Jacometti	7
Marzotto	1969	Mara/Impeto	6
Libellula	1970	Tevere/Giuliari//San Pastore	6
Irnerio	1970	Produttore/Manitoba	13
Manital	1981	Mendos/Marzotto	13
Centauro	1983	Strampelli x Irnerio	13
Eridano	1989	Irnerio/Sper X	13
Lampo	1994	Manital/Liocorno	11

^a The data of quality score have been calculated by Pogna et al. (1989). The quality score can range from a minimum of 4 to a maximum of 17 and is based on the effects of individual HMW glutenin subunits bands or pairs of bands on gluten quality as determined by alveograph test. The scores assigned to individual bands or pairs of bands are then summed to calculate the quality score of a subunit composition.

(4-hydroxy-3,5-di-hydrobenzonitrile) at 0.291 ha^{-1} with Mecopront ((*RS*)-2-(4-chloro-*o*-tolylxy)propionic acid) at 0.651 ha^{-1} .

The recorded data include heading date (expressed in days from 1st April), plant height measured at spike neck (cm) (Zadoks-scale 7.0), lodging (expressed in percentage plot acreage), grain yield (kg ha^{-1} at 13% moisture), 1000-kernel weight (g) and hectolitic weight (kg hl^{-1}). At harvest three sub-samples of 1 m linear row of whole-plant were randomly collected from each plot to determine total dry matter, relative grain yield and, hence, the HI and kernel number per square meter. The N percentage of grain was determined after Kjeldahl's micro-method, followed by colorimetric reading with an automatic CLA analyzer (Carlo Erba, Milan, Italy).

Seed protein concentration was calculated by multiplying N by 5.75. Total-N grain uptake (N_g) as kg ha^{-1} was calculated by multiplying total grain yield by N percentage. The following parameters were calculated according to Novoa and Loomis (1981) and Craswell and Godwin (1984):

- (1) Apparent nitrogen recovery (AR_F) (%) as the ratio of (N_g uptake at $N_x - N_g$ uptake at N_0) to applied N at N_x .

- (2) Physiological efficiency (P_E) (kg per kg): as ratio of (grain yield at $N_x - \text{grain yield at } N_0$) to (N_g uptake at $N_x - N_g$ uptake at N_0).

- (3) Agronomic efficiency (A_E) (kg per kg): as the ratio of (grain yield at $N_x - \text{grain yield at } N_0$) to N applied at N_x .

To evaluate the bread-making quality of the different cultivars, grain samples from each plot were individually milled with a Bona 4RB experimental mill (Bona, Monza, Italy). Flour quality was evaluated in terms of gluten strength (W) and the ratio between resistance (P) and extensibility (L) of dough as determined after ICC method 121 (1992) using the Chopin alveograph.

2.1. Weather conditions

The minimum and maximum temperatures and rainfall were in line with the 30-year averages in 3 of the 4 trial years. One year, 1995, registered a marked temperature drop in early May, i.e. approaching 0°C , at heading-anthesis stage, with the consequent adverse effect on spike fertility; this year also had above-average rainfall during the growing season, i.e. 766 mm total or 38% above the 30-year average

(486 mm). Most rain occurred in May, i.e. 224 mm or 218% above the 30-year average (70 mm) for the same month.

2.2. Statistical analysis

ANOVA was carried out taking years as non-fixed effects (factors) and N-fertilization and cultivar as fixed effects. Year of release was considered a quantitative variable for measuring genetic grain progress. The results reported herein are those in which significant statistical differences were found.

3. Results

3.1. Grain yield and morphophysiological traits

Grain yield, HI, kernel number per square meter, 1000-kernel and hectolitic weight, heading date, plant height and lodging were significantly affected by year and N-rate (Table 2). The unseasonable heavy rains, which facilitated N-soil leaching, together with low temperatures, were largely responsible for the resulting low 1995 yield as well as the reason for the between-year differences and the “year \times nitrogen” and “year \times cultivar” interactions.

The highest yield was recorded in 1993, the year when almost all the other parameters tested also showed the best values; the maximum yield was recorded at N_{80} . Although the next scale-up in N-input (N_{160}) increased seed number per square meter, it did not lead to a significant grain yield rise as a result of the significant decrease in the HI and 1000-kernel weight with respect to the lower N-input rate N_{80}

(Table 2). The nitrogen effect was also evident on heading date, plant height and lodging index, with significantly higher values from N_0 to N_{160} (Table 2).

The cultivars and their interaction with N were significant for grain yield and all the other morphophysiological traits analyzed. Grain yield of cultivars (Table 3) more than doubled, going from the 3835 kg ha⁻¹ of Cologna Veneta, a population grown in the early 1900s, to the 7133 kg ha⁻¹ of Lampo, a cultivar released in 1994. The progression of cultivar yield capacity within this broad range shows an almost linear trend, with significant and particularly consistent yield increments over time for Autonomia B, San Pastore, Marzotto, Irnerio, Centauro and Lampo. This rise in yield was accompanied by a radical change in both yield components and plant morphophysiological traits. In fact, over time, the cultivars matured increasingly earlier, plant height was reduced, tolerance to lodging notably improved, the HI increased, kernel number per acreage unit more than doubled with respect to the old populations, and 1000-kernel weight dropped (Table 3).

The yield response of the tested cultivars improved progressively from the old populations to the modern varieties for all three N-input rates (Fig. 1). The ‘N \times cultivar’ interaction shows that cultivar grain yield over time was differently influenced by N-rate. The populations of the early 1900s had the same yield capacity at N_0 as those released up to 1930 but, unlike the latter, showed significant yield loss at the 80 kg ha⁻¹ N-input (N_{80}). By contrast for the first cultivars bred in the 1910s, Ardito and Villa Glori (1916, 1918), while maximizing yield at N_0 , evince decreases only at N_{160} ; beginning with Autonomia

Table 2

Effect of years and nitrogen rate on the mean value over 16 cultivars for grain yield (kg ha⁻¹), harvest index (%), kernel number per square meter, 1000-kernel weight (g), heading time (days from 1st April), plant height (cm) and lodging (score 0–9)

	Years				LSD _(0.05)	Nitrogen rate (kg ha ⁻¹)			LSD _(0.05)
	1993	1994	1995	1996		N_0	N_{80}	N_{160}	
Grain yield (kg ha ⁻¹)	5571	5373	5120	5364	71	4966	5544	5562	37
Harvest index (%)	46	43	40	43	0.5	43	44	43	0.2
Kernel number per square meter	14390	13256	12651	14199	188	12125	14145	14602	124
1000-kernel weight (g)	39	40	40	38	0.5	42	40	39	0.3
Heading date (days from 1st April)	35	34	39	38	0.5	34	36	39	0.3
Plant height (cm)	102	102	113	107	4	102	107	109	5
Lodging (score 0–9)	2	3	3	4	0.6	2	3	4	0.3

Table 3

Grain yield (kg ha^{-1}) harvest index (%), kernel number per square meter, 1000-kernel weight (g), heading time (days from 1st April), plant height (cm) and lodging (score 0–9) mean values for cultivars over years and nitrogen rate

Cultivar	Year of release	Grain yield (kg ha^{-1})	Harvest index (%)	Kernel per square meter (no.)	1000-kernel weight (g)	Heading time (days from 1 st April)	Plant height (cm)	Lodging (score 0–9)
Cologna Veneta	1900	3835	33	8149	47	44	143	8.5
Gentil Rosso	1900	3949	32	8456	47	46	144	8.2
Ardito	1916	4034	34	9608	42	42	138	8.2
Villa Glori	1918	4166	38	9773	43	37	125	7.8
Autonomia B	1930	4348	37	10068	43	35	124	5.4
San Pastore	1940	5484	39	13882	40	33	120	1.1
Mara	1947	5167	44	13754	38	35	93	0.9
Abbondanza	1950	5176	42	12559	41	35	118	4.6
Gallini	1956	5245	43	14063	37	34	99	2.4
Marzotto	1969	5588	49	15397	36	35	82	1.2
Libellula	1970	5687	48	14142	40	33	99	3.5
Irnerio	1970	6038	49	15921	38	34	88	0.6
Manital	1981	5977	50	14709	41	32	76	0.1
Centauro	1983	6883	51	18647	37	33	78	0.6
Eridano	1989	7006	50	18983	37	34	92	0.1
Lampo	1994	7133	52	19868	36	33	77	0.0
LSD _(0.05)		94	0.6	269	0.7	0.6	1	0.4

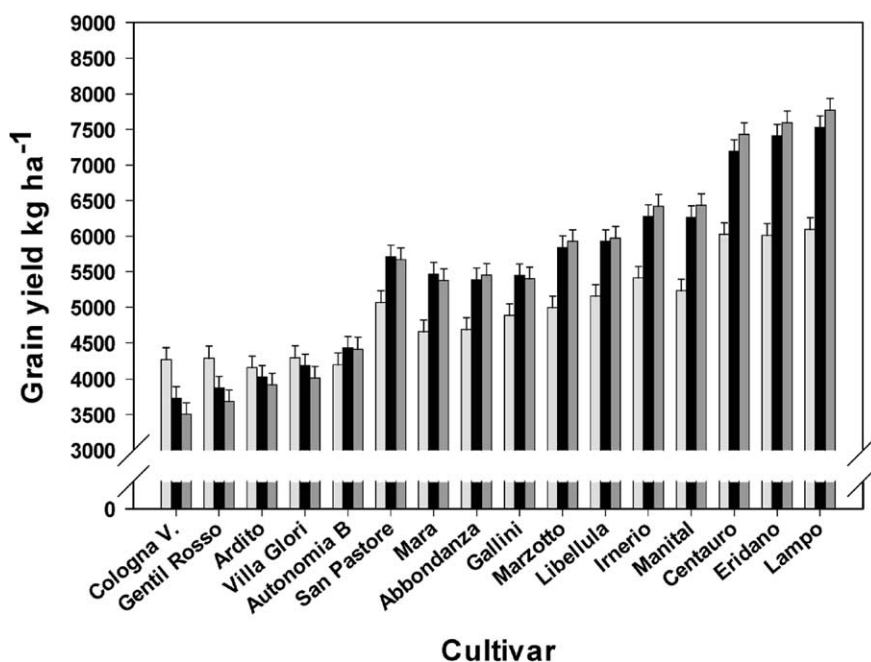


Fig. 1. Grain yield (kg ha^{-1}) mean value of 4 years for interaction nitrogen × cultivar. Legend of column: N_0 = □, N_{80} = ■, N_{160} = ▨. The bars on the top of the columns represent the $\text{LSD}_{(0.05)}$ for mean value comparison.

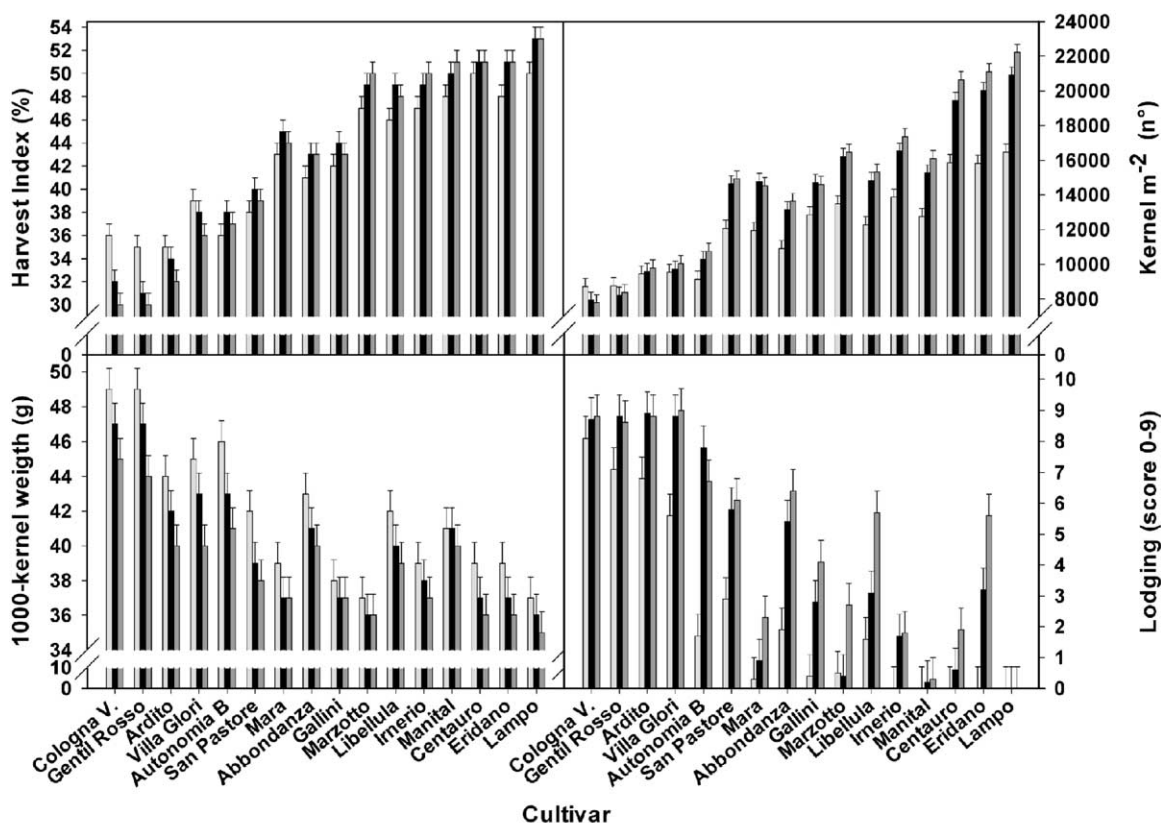


Fig. 2. Harvest index (%), 1000-kernel weight (g), kernel per square meter (no.) and lodging score mean value of 4 years for interaction nitrogen \times cultivar. Legend of column: N_0 = \square , N_{80} = \blacksquare , N_{160} = \square . The bars on the top of the columns represent the $LSD_{(0.05)}$ for mean value comparison.

B (1930) right up to Irnerio (1970), grain yield then optimized at N_{80} , while those developed thereafter (from Manital, 1981 to Lampo, 1994) maximized it at N_{160} (Fig. 1).

This differing N-effect on cultivar yield in relation to year of release is also found in all the other analyzed traits: the HI reached a peak values at N_0 for the old populations and for those developed between 1916 and 1918, at N_{80} for the cultivars bred from 1930 to the 1970s, and at N_{160} for those released between 1981 and 1994 (Fig. 2). Seed number per square meter generally showed a response similar to that found for the HI, although differing from it as did the trend recorded for Autonomia B, San Pastore and Abbondanza, bred respectively in 1930, 1940 and 1950, which had a higher seed number per square meter at N_{160} like the cultivars released from 1970 onwards. As expected,

1000-kernel weight dropped along with the N-input rate, but it did so at a different rate in relation to cultivar release date: at N_{160} it declined on average by 10% with respect to N_0 for the old populations up to San Pastore (1940) and, 2–5% in the cultivars released thereafter, the 7% decline for Abbondanza and Libellula being the sole exception.

Lodging was a particularly severe problem in the old populations and cultivars, the most susceptible being Cologna V., with an average 8.5 index and no significant difference in the N_0 to N_{160} range; Gentil Rosso, Ardito and Villa Glori had an average 8.2–7.8 rate range with significantly lower lodging at N_0 in comparison with N_{80} and N_{160} . The cultivars released after 1940, with the exception of Abbondanza, were increasingly less prone to lodging not only at N_0 but even at N_{80} ; lodging also significantly diminished at

Table 4

Nitrogen grain uptake (N_g) (kg ha⁻¹), apparent nitrogen recovery (AR_F), physiological efficiency (P_E) and agronomic efficiency (A_E) mean values for cultivars, nitrogen rate and their interactions

Cultivar	Year	N_g (kg ha ⁻¹)				AR _F (%)		P_E (kg per kg)		A_E (kg per kg)	
		N_0	N_{80}	N_{160}	Mean	N_{80}	N_{160}	N_{80}	N_{160}	N_{80}	N_{160}
Cologna Veneta	1900	113	108	105	102	0	0	0	0	0	0
Gentil Rosso	1900	116	114	110	114	0	0	0	0	0	0
Ardito	1916	101	99	99	101	0	0	0	0	0	0
Villa Glori	1918	107	106	105	103	0	0	0	0	0	0
Autonomia B	1930	104	115	117	111	14	8	21	16	3	1
San Pastore	1940	112	135	138	128	28	16	29	24	8	4
Mara	1947	110	133	136	126	28	16	36	28	10	5
Abbondanza	1950	111	133	139	128	27	17	32	27	9	5
Gallini	1956	107	129	135	124	27	17	26	19	7	3
Marzotto	1969	118	147	152	139	30	17	35	35	11	6
Libellula	1970	122	146	149	139	36	21	27	24	10	5
Irnerio	1970	114	139	153	136	31	26	35	25	11	6
Manital	1981	140	172	186	166	40	29	32	26	13	8
Centauro	1983	122	150	160	144	34	23	42	37	15	9
Eridano	1989	119	157	162	146	47	27	37	37	17	10
Lampo	1994	130	174	184	162	56	34	55	31	18	10
LSD (0.05)			4		3	5		4		2	
Mean		115	134	139	129	25	21	25	21	8	5
LSD (0.05)			2			3		0		0.6	

N_{160} in Mara and Marzotto (2.3, 2.7), Irnerio and Centauro (1.8, 1.9), Manital and Lampo (0.3, 0.0).

3.2. N-input efficiency

Table 4 shows the values for cultivar, N-rate and their interaction for the parameters total grain N-uptake (N_g), apparent nitrogen recovery (AR_F), nitrogen physiological efficiency (P_E) and agronomic efficiency (A_E). N_g progressively increases from the old populations and early-century varieties to the cultivars of the late 1900s. Similarly, the amount of N_g increased as a function of N-rate from N_0 to N_{160} . The ‘N-rate × cultivar’ interaction showed that the old populations and the cultivars released before the 1930s were unable to increase N_g as its soil supply increased. The cultivars bred between the 1930s and the 1970s (Libellula) register a peak N_g at N_{80} ; while all the cultivars bred thereafter reach maximum N_g at N_{160} . Noteworthy, in this latter group are Manital, a cultivar bred in 1981 exhibiting the highest N_g peak at all three N-rates, and two cultivars Irnerio (1970) and Eridano (1989), both showing a N_g peak at N_{160} and at N_0 the same N_g as the early-century old populations.

The apparent nitrogen recovery (AR_F) in grain was on average 25% at N_{80} and 21% at N_{160} . The utilization of supplied N beginning only with Autonomia B (1930). Apparent nitrogen recovery (AR_F), from the latter, increased progressively for all cultivars up to a peak of 56% at N_{80} and 34% at N_{160} for Lampo. This enhanced use of N-supply is also underscored by the plant’s greater physiological efficiency (P_E). Starting from Autonomia B (1930), P_E , which at N_{80} and N_{160} was able to produce 21 and 16 kg grain, respectively, per kg N actually taken up, with Lampo rises at values of N_{80} and N_{160} of 55 and 31 kg grain per kg N actually taken up. Most of the cultivars, for this trait, showed values declining as N-supply rose, the exceptions Marzotto, Libellula and Eridano having statistically equivalent values as the rate increased.

Agronomic, or N-use, efficiency (A_E) improved progressively, from the old populations unable to use any N-input to the late 20th-century cultivars capable of 18 (at N_{80}) and 10 (N_{160}) kg grain per kg N-input used. Although agronomic efficiency diminished as N-supply rose, the ‘N-input rate × cultivar’ interaction was highly significant, a fact indicating how the cultivars increased their demand for nitrogen over time.

Table 5

Hectolitic weight (kg hl⁻¹), grain protein (%), alveogram *W* ($\times 10^{-4}$ J), alveogram *P/L* mean values for cultivars and years over nitrogen rate

	Year of release	Hectolitic weight (kg hl ⁻¹)	Grain protein (%)	<i>W</i> ($\times 10^{-4}$ J)	<i>P/L</i>
Cultivar					
Cologna Veneta	1900	74	16.0	79	0.35
Gentil Rosso	1900	73	16.1	65	0.38
Ardito	1916	72	14.0	67	0.65
Villa Glori	1918	76	14.2	71	0.25
Autonomia B	1930	78	14.2	106	0.26
San Pastore	1940	75	13.0	71	0.25
Mara	1947	77	13.4	96	0.30
Abbondanza	1950	79	13.5	130	0.28
Gallini	1956	76	13.1	132	0.31
Marzotto	1969	76	14.0	134	0.29
Libellula	1970	77	13.4	82	0.31
Irnerio	1970	77	12.3	171	0.39
Manital	1981	77	15.3	241	0.48
Centauro	1983	76	11.4	203	0.44
Eridano	1989	79	11.4	174	0.47
Lampo	1994	75	12.4	200	0.52
LSD _(0.05)		0.4	0.2	10	0.02
Years					
1993		79	13.3	138	0.36
1994		76	13.5	123	0.37
1995		74	12.6	114	0.39
1996		76	13.4	124	0.36
LSD _(0.05)		0.5	0.1	5	0.01

For example, the four most recently released cultivars showed A_E values that were not only high at N_{80} but that at N_{160} did not differ statistically from those recorded by the cultivars released between 1940 and 1970 at N_{80} .

3.3. Grain quality

Table 5 shows the hectolitic-weight values, grain protein concentration and bread-making traits for flours estimated by Chopin alveograph (*W* and *P/L*) for the cultivars over the years. Hectolitic weight showed year-linked variations ranging from 79 to 74 kg hl⁻¹; inter-cultivar differences appear more linked to the individual genotype than to the release date. Indeed, excluding the local populations and Ardito (1916) whose hectolitic-weight values were the absolute lowest, all the other cultivars showed values from 75 to 79 kg hl⁻¹, the peak being recorded for Abbondanza (1950) and Eridano (1989). Grain protein concentration showed a decreasing trend over

time of release, dropping from 16.1 to 11.4%, from the old populations to the more recent cultivars. Only Marzotto (1969) and Manital (1981) represent exceptions (14 and 15.3%, respectively).

The alveograph's *W*-index (flour quality) was clearly affected by year and cultivar. Here the cultivars showed a net improvement beginning with Abbondanza ($W = 130 \times 10^{-4}$ J) and with a peak with Manital ($W = 241 \times 10^{-4}$ J). Noteworthy among the cultivars released since 1970 is Libellula, a typical biscuit variety, which registered $W = 82 \times 10^{-4}$ J. The *W*-index data are corroborated by the dough-gluten properties (*P/L*), the values clearly influenced by genotype. While Ardito (1916) showed the highest absolute value (0.65), overall the *P/L* scores tended to rise over time, reaching values well beyond 0.40, beginning with the cultivars developed after 1970, up to 0.52 with Lampo (1994).

For all the quality parameters assayed, the 'cultivar \times N-input rate' interaction was significant (Fig. 3). Average hectolitic weight decreased from N_0 to

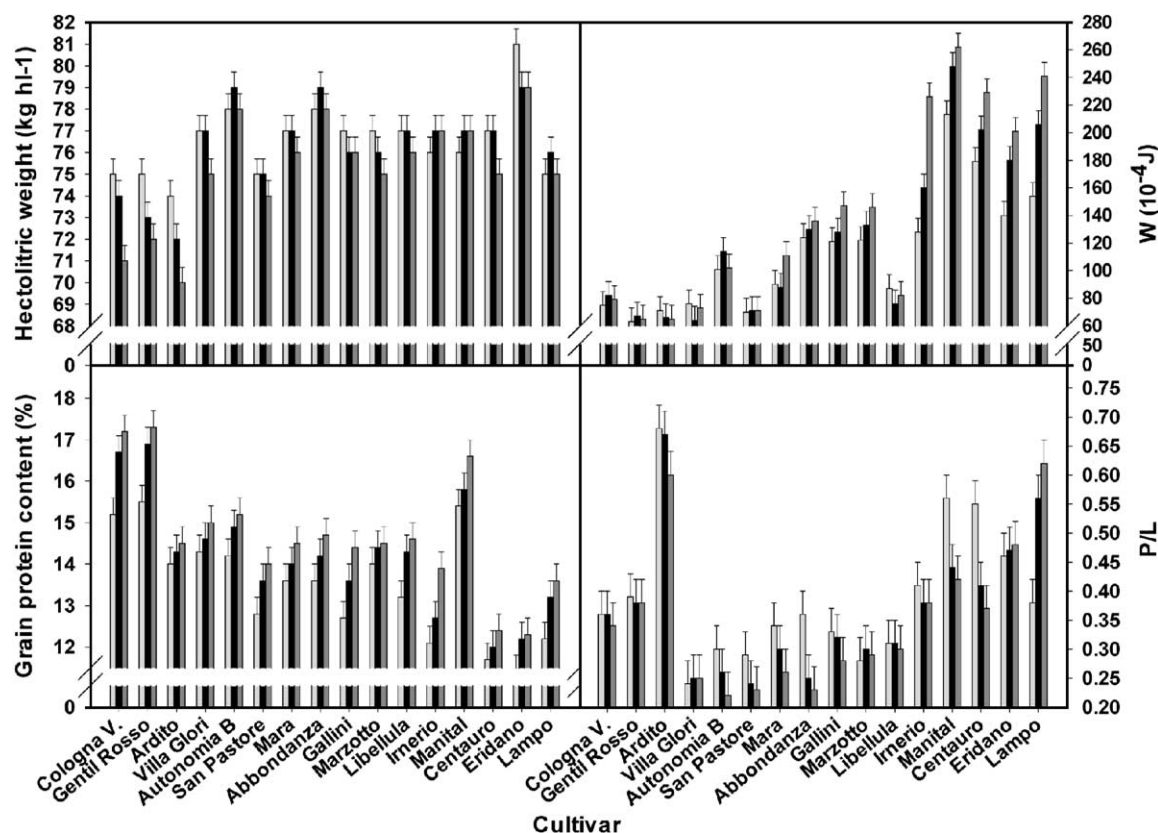


Fig. 3. Hectolitic weight (kg hl^{-1}), grain protein concentration (%), alveogram W ($\times 10^{-4}$ J), alveogram P/L mean value of 4 years for interaction nitrogen rate \times cultivar. Legend of column: N_0 = \square , N_{80} = \blacksquare , N_{160} = \square . The bars on the top of the columns represent the $\text{LSD}_{(0.05)}$ for mean value comparison.

N_{160} , an effect most evident in the early-century local populations and cultivars, although this trend levels off in the more recently bred cultivars and in those like Innerio and Manital there was even a significant improvement from N_0 to N_{80-160} . Grain protein concentration rose albeit differentially among the cultivars, along with N-rate. For example, the Cologna V. population and Mara, Abbondanza, Gallini, Innerio and Manital registered the highest levels only at the highest N-input (N_{160}) whereas the other cultivars recorded the highest protein concentration already at N_{80} . The 'N-rate \times cultivar' interaction for the W -index showed a particular response by the cultivars released after 1970: together with Gallini (1956), they registered a significantly better W -value as N-input rose. For the P/L ratio, the cultivar response to N-input variation showed that the old populations and

early-century varieties did not increase this value at rising N-supply and in most cases scored poorly and that the more recently bred cultivars scored decidedly better. Most of the cultivars optimized this parameter at N_0 , except for Lampo's which showed its peak at N_{160} .

4. Discussion

Our overall data indicate that the progressive bread-wheat yield gain recorded over the span 1900–1994 are largely dependent on cultivars and on their ability to use nitrogen inputs. The average yield rise throughout the trials was 33.5 kg ha^{-1} per year, a finding in line with the data reported by Canevara et al. (1994). This improvement is the result

of the progressive remodeling of plant architecture by breeders, which has led, on the one hand to reduced plant height, thereby enhancing resistance to lodging and optimizing the growth cycle with earlier heading, and on the other hand to higher spike fertility and improved partitioning of kernel-assimilated photosynthates—characteristics that resulted in a rise of kernel number per unit of acreage (an average 114 kernels ha^{-1} per year) and of HI (0.22% per year). This represents an evolution in the traits of Italian cultivars that is similar to those in other countries in Europe and elsewhere (Austin et al., 1980; Waddington et al., 1986; Cox et al., 1988; Feil, 1992; Slafer et al., 1994).

The selection carried out for all these traits also played a key role in upgrading the intrinsic efficiency for N-use of the cultivars developed since the early 1900s and the average capacity to store N in grain proteins. Our findings show that over time the increase in grain N-accumulation was 0.21 kg ha^{-1} per year without N-inputs and 0.67 and 0.82 kg ha^{-1} per year at 80 and 160 kg ha^{-1} N-inputs, respectively, thereby underscoring differences over supply rates but not in the respective slope. This increase in N-uptake is matched by average yield increments of 44, 50 and 47 kg per kg of N-accumulated. These data indicate that, despite performing selection under optimum N-supply conditions, cultivar evolutionary trend has led to a progressive improvement of the N-assimilation capacity regardless of N-supply, as reported also by Ortiz-Monasterio et al. (1997). At no nitrogen input the gain in grain yield was 19 kg ha^{-1} per year while at 80 and 160 N rate ha^{-1} the recorded gains were 39 and 43 kg ha^{-1} per year, respectively.

These figures indicate that the cultivars employed in our trials exhibited a progressive rise in demand for N-supply over time of release so as to maximize yields. This is, as shown by the ‘nitrogen \times cultivar’ interaction; in fact, beginning from the yield optimization at no N-input by the early-century populations and varieties, we come to cultivars that register their peak yield at the N-rate of 80 kg ha^{-1} and subsequently to those released after the 1970s that maximize yield at the N-rate of 160 kg ha^{-1} . The progressive rise in N-accumulation is also corroborated by the upgraded capacity of N-use (AR_F), by the yield enhancement in relation to the nutrient taken up by the crop (P_E)

and in the plant’s ability to increase yield in response to N-supply (A_E). The apparent N recovery fraction (AR_F) registered a notable rise in response to an average yearly increment of 0.54 and 0.35% at the respective N_{80} and N_{160} input rates, and this improvement in the cultivars is likely attributable to the enhanced uptake capacity following input. The rise in AR_F appears to be an indirect result of breeding as there is some evidence suggesting that it is imputable to differences in root system traits (Lupton et al., 1974; Barraclough, 1989). Foulkes et al. (1998) attribute it to the tendency of modern cultivars to develop a few early rather than late tillering culms, which would result in little N-soil recovery on the one hand while the extended tiller life-span on the other means that peak N-demand occurs in the early plant development when N-input is the main source of supply. This would explain the reduced uptake in early development to the benefit of an extended late uptake linked to N-supply (Delogu et al., 1998), which also translates into greater agronomic (A_E) and physiological (P_E) efficiency. Indeed, the progressive upgrade in the latter two parameters was respectively 0.19 and 0.50 kg grain per year at N_{80} and 0.11 and 0.39 kg grain per year at N_{160} .

The rise in yield and the enhanced N-use found over time proved to be coupled to diminished grain protein concentration. This protein drop, which was 0.03% per year, appears not to be linked to direct genetic effects but to a dilution effect in the amount of proteins due to an increase in the amount of carbohydrates (Kibite and Evans, 1984): indeed, protein production per hectare from the oldest to the latest cultivars actually increased by 13, 37 and 43% at N_0 , N_{80} and N_{160} , respectively. This suggests a close link between protein and carbohydrate storage in seed and that it keeps the seed N-concentration relatively stable. Austin et al. (1980) note that the nitrogen HI is very stable with respect to both HI and seed N-concentration, indicating the possibility of further enhancing cultivar yield capacity at the current N-level.

Yet this lower grain protein concentration of the cultivars over is matched by a quality improvement in protein composition. All the tested cultivars released after 1970 had a rating above 10 in quality score (Pogna et al., 1989). The enhanced quality traits of these bread-wheat cultivars over time is also underscored by the W and P/L parameters, which respectively rise

from values between 65–170 and 0.25–0.39 per cultivar from 1900 to 1970 to 174–241 and 0.48–0.52 for those released after 1970. In fact, the rising trend found over time for the *P/L* ratio is also evident at no N-input, i.e. when this ratio is optimized, whereas at high N-inputs the value of *W* is optimized, thereby underscoring an overall enhanced use of N-supply in the modern cultivars. These findings show that over the last century the goal of upgrading both yield amounts and grain quality for bread-making was successfully achieved.

This success also indirectly led to improved plant nitrogen uptake and use, clear indicators that even in conditions of limited inputs or under organic-farming practices the best results are to be attained by employing not old populations or varieties but modern cultivars, the latter being the only ones with the intrinsic traits capable of ensuring yield and quality at low N-supply even though they maximize their traits at high nitrogen inputs. However, the ever-pressing demand for a sustainable agriculture of low environmental impact and the continuing spread of organic-farming mean that in the third millennium breeders must focus more effort on the plant's morphological and physiological traits to develop cultivars endowed with resistance factors to biotic and abiotic sources of stress and of enhanced nutrient efficiency. This implies on the one hand assigning greater importance to selection under conditions of limited inputs and organic agriculture and on the other prioritizing the available sources of variability.

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