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Breeding progress in grain yield of winter wheat cultivars grown at different nitrogen levels in semiarid conditions

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The objectives of this study were to estimate the progress in wheat genetic yield potential, associated with changes in some agronomic traits, under different N rates. Twenty-four cultivars of winter wheat (*T. aestivum* L.) representing most of the cultivars released in Serbia from 1955 to 2006 were analyzed. The cultivars were grown for four years (2005–2008) in field trails with two levels of agronomic inputs (low nitrogen-N_{45} and high nitrogen-N_{110}). Data were collected on 1000-kernel weight, kernels per spike, kernels per square meter, spikes per square meter, plant height, harvest index, heading time and grain yield. Mean difference between the two fertilization levels was 0.44 t ha^{-1}. The average rate of increase in yield potential per year of release, estimated from the slope, was 41 kg ha^{-1} $year^{-1}$ and it was significantly different from zero ($P \leq 0.01$). It was 35 kg ha^{-1} $year^{-1}$ or 0.55% at the low level of N input, and 46 kg ha^{-1} $year^{-1}$ or 0.68% at the high level of N input. This suggests that modern cultivars are better adapted to high N input. Our results suggested that individual contribution of the most of analyzed traits may vary depending on the genotype as well as environmental conditions.

Key Words: breeding, cultivars, nitrogen, wheat, yield, yield components.

Introduction

Wheat yield increases depend for the most part on the cultivars grown, climatic conditions and the growing technologies used. Increases in the genetic potential for yield of new cultivars and the improvement of other agronomic and technological traits make it possible to increase wheat production per unit area.

Up until the mid-1950s, wheat cultivars grown in the former Yugoslavia were mostly those originating from the native populations. These cultivars were characterized by good winter hardiness, thin and tall straw, late maturity and low productivity. During that period, breeding was mostly confined to mass and individual selection from the native populations. Modern wheat breeding in former Yugoslavia began in the second half of the 1950s (1956/57), when three centres for the advancement of wheat breeding and production were founded in the cities of Novi Sad, Kragujevac and Zagreb (Borojević 1990). The main strategy for plant breeding programs aimed at better grain yield, shorter stature and early maturity. The history of Serbian wheat breeding can be divided into several distinct phases depending on which kind of breeding material was used. In the beginning, the most common crosses were those among genetically divergent foreign cultivars, with one of the parents being of the intensive type (Misic and Mladenov 1998). The second phase was characterized by crosses between various foreign cultivars and high-yielding cultivars developed during the previous phase. In the third phase, genetically divergent domestic cultivars and lines were crossed among themselves in order to accumulate as many desirable genes as possible. The current period is marked by the search for sources of genes and ways to surpass the yield levels of the existing cultivars. This includes the use of hybridization of the most productive foreign and domestic genotypes of wheat.

In Serbia as well as in most other countries, average wheat yields are significantly higher today than 40–50 years ago (Brancourt-Hulmel *et al.* 2003, Donmez *et al.* 2001, Guarda *et al.* 2004, Slafer and Andrade 1989). Tremendous progress has been achieved in Serbia wheat production, and the national average yield has increased from 1.06 t ha^{-1} in 1956 to 4.30 t ha^{-1} in 2008. This has been largely due to the development of new cultivars and improvements in crop management practices. Between 1955 and 1991, commercial wheat yields increased in Serbia at a rate of 90 kg ha^{-1} per year on average. In period between 1992 and 2008 national gain of winter wheat in Serbia was increased only 22 kg ha^{-1} per year. Results of other authors have shown that national gains (in different countries) were increased from 28 to 135 kg ha^{-1} per year, while the genetic gains for grain

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yield varied from 5.8 kg ha^{-1} per year to 59.0 kg ha^{-1} per year (Brancourt-Hulmel *et al.* 2003). Although it is difficult to determine precisely the relative contributions of cultivar, cultural practice and climatic factors to the global increase of wheat yields, it can be said that the first of the three factors have played the dominant role in this regard (Austin *et al.* 1980, Evans and Fischer 1999). In the last two decades, however, wheat yields in Serbia have been far below the genetic potentials of the domestic cultivars and the possibilities offered by the climatic and edaphic conditions in the country. This has been partly due to unfavourable weather conditions (most of the years were either droughty or characterized by an unfavourable distribution of precipitation), but the most important reason by far have been unfavourable economic factors, especially during the 90's.

Our study was undertaken with the following objectives: (i) to estimate the progress made in improving the genetic yield potential of wheat, (ii) to examine changes in some agronomic traits associated with genetic yield potential improvement and (iii) to evaluate expression of yield potential under different N rates. This could provide valuable information for further improvement of grain yield and determination of future strategies for breeding programs in Serbia and elsewhere.

Materials and Methods

Agronomical trials

The study was carried out at the experimental field of the Institute of Field and Vegetable Crops, Novi Sad, Serbia (45°33′N, 19°85′E, 82 m altitude) for four consecutive growing seasons (2005–2008). The location is characterized by semiarid conditions, with dry, hot spring and summer, neutral autumn and moderately cold winter. Each year the plots were rotated with soybean (*Glycine max* L.). The soil type was Chernozem Chernic (FAO, Rome, 1998).

The wheat cultivars were planted in a randomized complete block design with three replicates. Each plot consisted of 10 rows, 10 cm apart and 5 m long (harvested area was 5 m^2). Seedling density was considered 500 seeds m^{-2}. All the trails were seeded in middle October (optimum sowing date) and reached maturity in late June or early July. Weeds were controlled by hand.

Two different levels of agronomic inputs were applied: (i) low nitrogen (N_{45}); (ii) conventional nitrogen (N_{110}), representing the standard agronomic condition applied by farmers in Serbia and where the genotypes could express their yield potential. In the low nitrogen treatment 45 kg ha^{-1} of N fertilizer (NPK, 15 : 15 : 15, 300 kg ha^{-1}) were applied in one rate and incorporated prior to sowing date. For conventional nitrogen treatment 110 kg ha^{-1} of N fertilizer were applied in two rates: 45 kg ha^{-1} before sowing date (NPK, 15 : 15 : 15, 300 kg ha^{-1}) and 65 kg ha^{-1} (calcium ammonium nitrate, N 27%) at tillering stage (end of February or beginning of March).

Cultivars

Twenty-four cultivars of winter wheat representing most of the cultivars released in Serbia from 1955 to 2006 were used in the study. Because of the many years that elapsed between the introduction of Banatka and Bankuty 1205 and the first release of winter wheat cultivars arising from breeding programs, we used the year 1955-during the period when winter wheat breeding programs were getting underway. Only cultivars sharing more then 20% of wheat area in the Serbia were included in the trials. Banatka is native population, Bankuty 1205 is old Hungarian, San Pastore and Libellula are Italian, Bezostaja 1 is worldwide famous old Russian, Zlatna Dolina is Croatian and Skopljanka is FYR Macedonian. Serbian cultivars used in the study were created in two breeding centres, Small Grains Research Centre, Kragujevac (Kragujevacka-56) and Institute of Field and Vegetable Crops, Novi Sad (Sava, Partizanka, Novosadska rana 2, Balkan, Yugoslavia, Lasta, Evropa 90, Pobeda, Novosadska rana 5, Renesansa, Pesma, Ljiljana, Cipovka, Dragana, Simonida and NS 40S). The cultivars released after 2000th were included in the study in order to represent the next generation of yield improvement.

Morphological and agronomical traits

Heading time (HT), plant height (PH), lodging (LG) and number of spikes per square meter (SPM) were recorded during the vegetation period. Heading time was calculated as the number of days after January 1st to the heading date. Heading date was recorded at the day when at least 50% of the spikes in a plot had emerged fully (growth stage 55; Zadoks *et al.* 1974). Plant height in centimeters (cm) was measured during the milk-waxy maturation, from the soil surface to the top of the spikes (awns excluded) of three random plants sampled from the middle rows of each plot. Lodging (%) was estimated before harvest by the degree and amount of plants that lodged per plot. The number of spikes per square meter was calculated by counting the spikes in 1 m of one of the central rows in each plot. The subsample consisting of 30 single plants (10 plants per replicate) from inside the plots was used for the yield components analysis. Number of kernels per spike (KPS) was determined by counting kernels on every spike. Harvest index (HI) was calculated as a ratio (%) between grain yield and above-ground biological yield at physiological maturity. Thousand kernels weight (g) (TKW) was calculated as the mean weight of three sets of 100 grains from each plot. The number of kernels per square meter (KPM) was calculated by multiplying SPM by the KPS. Grain yield (YLD) was measured by harvesting the all ten rows of each cultivar for each replicate (expressed in t ha^{-1} at 13% moisture).

Statistical analysis

Statistical analysis was conducted for each parameter by analysis of variance (ANOVA) in a factorial design with 4 years, two levels of agronomic inputs and 24 cultivars. Cultivar and N levels were considered fixed factors and

Table 1. Analysis of variance (significance) of grain yield and agronomical traits of 24 wheat cultivars grown in 2005, 2006, 2007 and 2008 seasons at Novi Sad

Source of Variation	Traits[a]								
	df	YLD	TKW	KPS	SPM	KPM	PH	HI	HT
Year (Y)	3	**	**	**	**	**	**	**	**
R (Y)	8	ns	ns	ns	ns	ns	ns	ns	ns
Level of N	1	**	**	**	**	**	**	**	**
Y × N	3	**	**	**	**	**	**	**	**
Cultivar (C)	23	**	**	**	**	**	**	**	**
Y × C	69	**	**	ns	**	**	**	ns	**
N × C	23	**	**	**	**	**	**	**	ns
Y × N × C	69	ns	**	ns	**	**	ns	ns	**

[a] YLD = grain yield, TKW = 1000 kernels weight, KPS = kernels per square meter, SPM = spikes per square meter, KPM = kernels per square meter, PH = plant height, HI = harvest index, HT = heading time.

Level of statistical significance: * $P < 0.05$; ** $P < 0.01$; and ns: not significant.

years random (Carmer *et al.* 1989). Least significant difference (LSD) values were calculated using Mstat-C Version 2.0 Software (Michigan State University, MI, USA).

The year of cultivar 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. Regressions were performed with SPSS computer software. Genetic gains were estimated by several means per cultivar: the grand mean, mean per low N and mean per high N.

Results

Grain yield

Genetic variation for grain yield was highly significant ($P \leq 0.01$), as expected from a diverse genotypic sample spanning nearly 50 yr of genetic improvement (Table 1). Growing season significantly ($P \leq 0.01$) affected grain yield in both production treatments. The combined analysis for grain yield produced significant ($P \leq 0.01$) interaction between N levels and cultivar (N × C) and year and cultivar (Y × C) (Table 1). The N × C interaction mean squares for grain yield was greater than for the Y × C interaction (data not shown), implying that genotypes were more sensitive to N level than to years. The three-way interaction (Y × N × C) for grain yield was not significant. Great yield was only partly due to the cultivar improvement, since the genotype mean square was smaller than the treatment mean square. The improvement was also a consequence of different interactions, the most important being the interactions with treatment (Table 1).

The mean yield at low N was 6.26 t ha^{-1}; yield ranged from 4.81 t ha^{-1} for Banatka old native population to 7.37 t ha^{-1} for Simonida released in 2003 (Table 2). The mean yield at high N was 6.80 t ha^{-1}; yield ranged from 4.87 t ha^{-1} for Bankuty 1205 old Hungarian cultivar to 7.81 t ha^{-1} for NS 40S released in 2006. Mean difference (0.54 t ha^{-1}) between the two fertility levels was significant ($P \leq 0.01$). Mean grain yield across for growing seasons and two production treatments was 6.53 t ha^{-1}. Grand yield significantly varied among cultivars ranging from 4.86 to 7.56 t ha^{-1}. The lowest yielding cultivars were Banatka which did not significantly different from other old cv Bankuty 1205. Grain yield of cultivars released thereafter exhibited a significant trend to increase with the year of release and Simonida, Dragana and NS 40S were the highest yielding cultivars with 7.56, 7.41 and 7.39 t ha^{-1}, respectively. Considering the best value obtained per year, the yield of some cultivars exceeded 8.5 t ha^{-1} (data not shown). Of the ten highest yielding cultivars, four were released in a period from 2000 to 2006 (Simonida, Dragana, NS 40S and Ljiljana), five were released in a period of 1990–1999 (Pobeda, Renesansa, Pesma, Evropa 90 and NS rana 5) and only one was released from 1980 to 1989 (Lasta).

The average rate of increase in yield potential per year of release estimated from the slope of the graph was 41 kg ha^{-1} $year^{-1}$ and it was significantly different from zero ($P \leq 0.01$) (Table 2). The relative annual genetic yield gains of wheat cultivars over 50 years, was 0.62%. It varied from 35 kg ha^{-1} $year^{-1}$ or 0.55% at the low level of N input, to 46 kg ha^{-1} $year^{-1}$ or 0.68% at the high level of N input (Fig. 1). Grain yield showed a significant and positive correlation with year of release (Table 2)

Yield components

Kernels per spike, spikes per square meter, 1000-kernel weight and kernels per square meter were significantly ($P \leq 0.01$) affected by year, N-level and cultivar (Table 1). Moreover, for all the yield components assayed, the N-level × cultivar and year × cultivar interactions were significant, except the Y × C for kernel per spike.

Among yield components, kernels per square meter increased throughout the half century ranging from 12094 of Banatka to 19490 kernels per square meter of NS 40S. The increase in kernels per square meter was associated with an increase in kernels per spike and increase in spikes per

Table 2. Mean of 24 wheat cultivars at two N levels, across four years for grain yield, 1000-kernel weight, kernels per spike and kernel per square meter

Cultivar	Code	Year of release	Grain yield			1000-kernel weight			Kernels per spike			Kernel per square meter		
			low N	high N t ha^{-1}	mean	low N	high N g	mean	low N	high N No.	mean	low N	high N No.	mean
Banatka	BA	1955	4.81	4.92	4.86	40.3	39.9	40.1	21.9	22.1	22.0	11909	12280	12094
Bankuty 1205	BN	1955	4.93	4.87	4.90	40.3	40.1	40.2	21.8	21.8	21.8	12015	12225	12119
San Pastore	SP	1958	5.39	5.52	5.46	38.7	38.4	38.5	24.3	24.8	24.6	13780	14535	14158
Bezostaja 1	BE	1959	5.74	5.81	5.77	42.8	40.9	41.7	24.0	24.7	24.4	13290	14290	13789
Libellula	LI	1962	6.15	6.33	6.24	41.6	41.0	41.3	25.9	26.7	26.2	14606	15614	15110
Sava	SA	1970	6.00	6.71	6.35	39.2	39.9	39.5	27.0	27.9	27.4	15302	16810	16056
Zlatna Dolina	ZD	1970	5.95	6.78	6.36	39.5	38.8	39.2	26.6	28.3	27.5	15059	17301	16180
Partizanka	PA	1973	5.92	6.46	6.19	41.2	39.7	40.5	26.5	27.2	26.9	14284	16304	15294
NS rana 2	N2	1975	6.11	6.67	6.39	41.6	40.6	41.1	26.6	27.2	26.9	14799	16423	15611
KG 56	KG	1975	6.10	6.59	6.34	42.7	41.1	41.9	26.0	27.1	26.5	14118	15866	14992
Balkan	BL	1979	6.26	6.84	6.55	42.2	41.7	42.0	26.3	27.5	26.9	14728	16402	15565
Yugoslavia	YU	1980	6.38	6.99	6.69	42.5	42.2	42.4	26.1	27.5	26.8	14840	16546	15693
Skopljanka	SK	1982	6.21	7.00	6.61	40.0	39.1	39.6	27.7	29.4	28.6	15406	18020	16713
Lasta	LA	1987	6.65	7.16	6.90	39.6	38.0	38.8	28.8	30.4	29.6	16600	18796	17698
Evropa 90	EU	1990	6.67	7.21	6.94	39.8	37.4	38.6	29.7	31.1	30.4	16702	19362	18032
Pobeda	PO	1990	6.65	7.43	7.04	40.7	39.2	40.0	29.1	31.0	30.1	16300	19120	17710
NS rana 5	N5	1992	6.40	7.25	6.82	40.1	39.0	39.6	28.3	30.2	29.2	16190	18660	17425
Renesansa	RE	1994	6.73	7.36	7.04	41.9	39.2	40.6	28.7	31.2	30.0	16000	18794	17397
Pesma	PE	1995	6.54	7.45	6.99	39.4	38.9	39.3	29.7	29.3	29.6	16570	19300	17935
Ljljiljana	LJ	2000	7.10	7.52	7.31	41.4	39.4	40.4	29.7	31.7	30.7	17420	19138	18279
Cipovka	CI	2002	6.11	7.24	6.67	40.0	38.9	39.5	27.6	30.3	29.0	15310	18691	17000
Dragana	DR	2002	7.18	7.64	7.41	42.7	40.7	41.8	29.4	29.6	29.5	16810	18900	17856
Simonida	SI	2003	7.37	7.76	7.56	41.9	40.7	41.4	30.2	31.8	31.0	17543	19175	18360
NS 40	NS	2006	6.97	7.81	7.39	39.2	37.0	38.0	30.8	33.0	32.0	17850	21130	19490
Mean			6.26	6.80	6.53	40.8	39.7	40.3	27.2	28.4	27.8	15310	17237	16273
Gain			0.035	0.046	0.041	0.00	−0.00	−0.00	0.14	0.16	0.15	88	130	109
Gain %			0.55	0.68	0.62	0.00	−0.00	−0.00	0.51	0.56	0.54	0.57	0.75	0.67
Level of significance-gain			**	**	**	ns	ns	ns	**	**	**	**	**	**
R^2			0.78	0.86	0.85	0.01	0.10	0.02	0.84	0.84	0.84	0.81	0.86	0.85
CV (%)			10.2	12.0	11.0	3.2	3.3	3.1	9.0	10.4	9.6	10.4	13.3	11.8
Correlation with year release			0.88	0.93	0.92	0.02	−0.32	−0.13	0.92	0.92	0.92	0.90	0.93	0.92
Level of significance-correlation			**	**	**	ns	ns	ns	**	**	**	**	**	**

Level of statistical significance: * $P < 0.05$; ** $P < 0.01$; and ns: not significant.

square meter and independent of consistent changes 1000-kernel weight, which did not exhibit a clear trend due to breeding improvements (Tables 2, 3).

Interaction between N-level and cultivar was significant for all yield components (Table 1). The nature of the interaction was explained by differences in slopes among N-levels (Tables 2, 3). Genetic gains in kernels per spike, kernels per square meter and spikes per square meter calculated for high N (0.22 kernels per spike per year, 144 kernels per square meter per year and 0.64 spikes per square meter per year, respectively) were always greater than the corresponding values of the low N (0.15 kernels per spike per year, 88 kernels per square meter per year and −013 spikes per square meter per year, respectively). 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: in newer cultivars 1000-kernel weight was more decreased then in older cultivars.

The number of kernels per spike, spikes per square meter and kernels per square meter were significantly associated with years of the cultivars release (0.92, 0.82 and 0.92, respectively). No significant association between 1000-kernel weight and years of release of cultivars (−0.13) was found.

Plant height, lodging, harvest index and heading time

A significant ($P \leq 0.01$) N-level × cultivar interaction was found for plant height (Table 1). Mean plant height of the wheat cultivars represented in this study was 99 cm at high-N and 93 cm at low-N (Table 3). Mean plant height across four growing seasons and two production treatments was 96 cm. Plant height decreased dramatically passing from 129 cm of cv Banatka selected from native population to 83 cm of modern cv Pesma. The modern cultivars carrying the dwarfing genes recorded plant height below 95 cm (Ljiljana, Cipvka, Dragana, Simonida, NS 40S). Estimated annual gain of plant height of cultivars, over the 50 years,

Table 3. Mean of 24 wheat cultivars at two N levels, across four years for spike per square meter, plant height, harvest index and heading time, while for lodging across three years

Cultivar	Code	Year of release	Spike per square meter			Plant height			Lodging			Harvest index			Heading time		
			low N	high N No.	mean	low N	high N cm	mean	low N	high N %	mean	low N	high N %	mean	low N	high N days	mean
Banatka	BA	1955	545	553	548	127	130	129	100	100	100	0.294	0.294	0.294	138	136	137
Bankuty 1205	BN	1955	550	560	555	127	131	129	91	99	95	0.308	0.306	0.307	134	132	133
San Pastore	SP	1958	568	584	576	98	105	102	72	96	84	0.374	0.370	0.372	123	125	124
Bezostaja 1	BE	1959	552	576	564	116	122	119	83	96	89	0.364	0.362	0.363	134	133	134
Libellula	LI	1962	565	585	575	94	98	96	39	69	54	0.408	0.410	0.409	131	130	131
Sava	SA	1970	565	605	585	85	92	89	4	6	5	0.420	0.432	0.426	127	126	126
Zlatna Dolina	ZD	1970	568	612	590	79	89	84	0	14	7	0.431	0.439	0.335	131	130	131
Partizanka	PA	1973	540	600	570	92	96	94	9	33	21	0.377	0.383	0.380	131	130	130
NS rana 2	N2	1975	555	605	580	89	97	93	3	11	7	0.397	0.403	0.400	127	127	127
KG 56	KG	1975	543	587	565	92	96	94	17	44	31	0.369	0.371	0.370	133	133	133
Balkan	BL	1979	558	598	578	89	92	91	0	10	5	0.418	0.424	0.421	133	132	132
Yugoslavia	YU	1980	567	603	585	94	99	97	11	36	23	0.410	0.424	0.417	132	132	132
Skopljanka	SK	1982	555	615	585	87	91	89	0	11	6	0.403	0.415	0.409	131	130	131
Lasta	LA	1987	575	621	598	84	90	87	0	26	13	0.407	0.413	0.410	132	132	132
Evropa 90	EU	1990	560	624	592	94	99	97	1	4	3	0.411	0.425	0.418	130	130	130
Pobeda	PO	1990	562	614	588	93	97	95	0	19	9	0.420	0.434	0.427	131	130	130
NS rana 5	N5	1992	570	620	595	87	92	90	0	11	6	0.400	0.416	0.408	127	128	127
Renesansa	RE	1994	556	604	580	83	90	87	0	13	7	0.417	0.429	0.423	129	128	128
Pesma	PE	1995	560	656	608	80	86	83	0	4	2	0.429	0.451	0.440	132	132	132
Ljljiljana	LJ	2000	584	606	595	92	96	94	1	14	8	0.450	0.476	0.463	128	127	127
Cipovka	CI	2002	553	619	587	88	92	90	2	19	11	0.452	0.472	0.462	128	127	127
Dragana	DR	2002	570	640	605	91	97	94	3	27	15	0.454	0.476	0.465	130	128	129
Simonida	SI	2003	580	605	593	88	93	91	0	16	8	0.465	0.490	0.478	128	127	127
NS 40	NS	2006	580	640	610	86	92	89	0	0	0	0.465	0.498	0.482	131	131	131
Mean			562	606	584	93	99	96	18	32	25	0.406	0.417	0.412	130	130	130
Gain			0.4	1.2	0.8	–0.48	–0.48	–0.48	–1.55	–1.58	–1.56	0.002	0.003	0.002	–0.05	–0.05	–0.06
Gain %			0.07	0.20	0.14	–0.52	–0.48	–0.50	–9	–5	–6	0.54	0.65	0.61	0.04	0.04	0.05
Level of significance-gain			**	**	**	**	**	**	**	**	**	**	**	**	ns	ns	ns
R^2			0.27	0.65	0.67	0.39	0.42	0.40	0.60	0.60	0.61	0.68	0.75	0.72	0.10	0.11	0.13
CV (%)			2.1	3.9	2.7	13.5	12.2	12.8	17.9	10.2	12.8	10.6	12.3	11.4	2.0	2.2	2.1
Correlation with year release			0.52	0.81	0.82	–0.63	–0.66	–0.65	–0.77	–0.77	–0.78	0.83	0.87	0.87	–0.30	–0.33	–0.36
Level of significance-correlation			**	**	**	**	**	**	**	**	**	**	**	**	ns	ns	ns

Level of statistical significance: * $P < 0.05$; ** $P < 0.01$; and ns: not significant.

was –0.49 cm and it was significantly ($P \leq 0.01$) different from zero. Plant height showed a significant and negative correlation with year of release (Table 3).

Remarkable reduction of height was already attained with Bezostaja 1 (119 cm) and with Libellula (96 cm) before wittingly introduction of the dwarfing genes from Akakomugi, the donor of Rht8 and Ppd1 genes. Bezostaja 1 came from very complex crosses in which one parent was Klein 33 from Argentina. Klein 33 came from a cross in which one parent was Ardito, of which one parent was Akakomugi (Borojevic and Borojevic 2005a). The pathway of the Rht8 gene (of the variety Akakomugi) was from Japan to Italy, from Italy to Argentina and from Argentina to Europe and the former Soviet Union. The source of Rht1 and Rht2 was the Japanese wheat variety Norin 10. Norin 10 was transferred from Japan to the United States after WWII and from the US to the CIMMYT in Mexico. From the CIMMYT, Rht1 and Rht2 genes were distributed all around the world, including Europe (Borojevic and Borojevic 2005a, 2005b).

In 2008 minor lodging occurred in most of the cultivars and that year was not included in the calculation. Other three years were used in overall lodging means to obtain regression and correlations with other traits. All sources of variation had significant effects on lodging. The cultivars differed in lodging from 100% for the old cv. Banatka to 0% for the new cultivar NS 40S (Table 3). Generally, when results for all cultivars were compared, lodging was significantly higher ($P < 0.05$) at high N (32%) than at low N-level (18%). The estimated average decrease in lodging of 1.56% per year, was between values obtained by Underdahl *et al.* (2008) 0.4% per year and Donmez *et al.* (2001) 2.15% per year. Comparison of the correlation coefficients between agronomic traits in

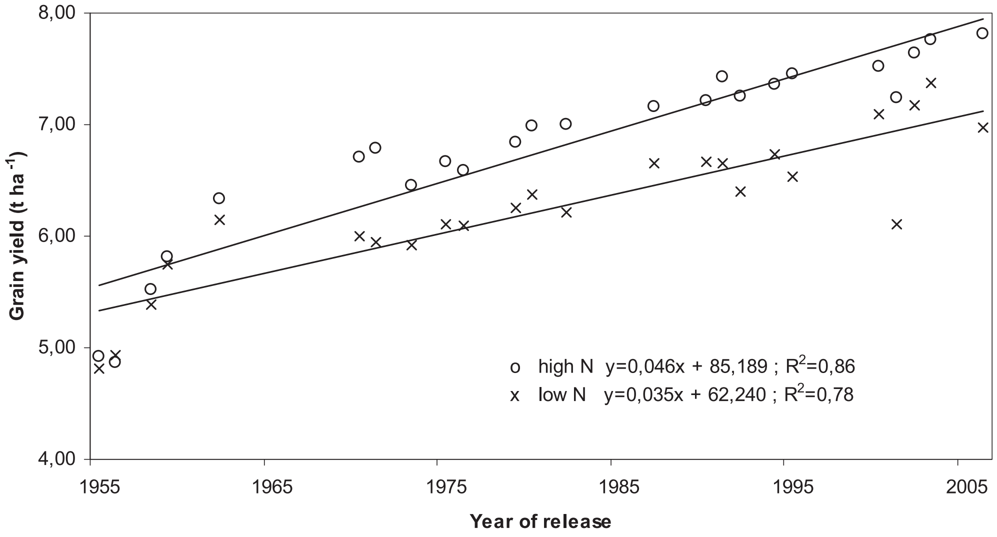

Fig. 1. Mean genetic progress of 24 wheat cultivars across four years at two levels of applied N

the two levels of N reveals no significant difference. In average for both N levels lodging showed a negative correlation with grain yield (r = –0.875, P < 0.01), kernels per spike (r = –0.854, P < 0.01), kernels per square meter (r = –0.783, P < 0.01), spikes per square meter (r = –0.789, P < 0.01), harvest index (r = –0.795, P < 0.01). However, lodging was positively correlated with plant height (r = 0.873, P < 0.01), and the heading time (r = 0.449, P < 0.05).

Harvest index was significantly (P = 0.01) affected by N-level and cultivar (Table 1). The cultivars differed in harvest index from 0.294 for the old cv. Banatka to 0.482 for the new NS 40S (Table 3). Generally, when results for all cultivars were compared, harvest index was higher at high N than at low N-level. The estimated average increase in harvest index of 0.25% per year is comparable to the 0.2% increase per year calculated by Brancourt-Hulmel *et al.* (2003) in wheat cultivars released in France from 1946 to 1992. The harvest index was positively correlated with years of release and grain yield (Table 3).

Mean of heading time of all wheat cultivars represented in the trial was 130 days. A combined analysis, averaged over N-level, indicated that there was no N-level × cultivar interaction for this trait (Table 1). The oldest cultivar Banatka, showed significantly (P ≤ 0.01) later heading time than all cultivars represented in the trial. Nevertheless, on both N-levels, modern cultivars were relatively similar in heading time with older cultivars. The genetic gain of heading time, over the past 50 years of breeding, was very low (–0.06 days per year) and was not significantly (P > 0.05) different from zero (Table 3). No significant correlation occurred between heading time and year of release for either individual or overall N-level (Table 3).

Association of grain yield and agronomic traits

In both N levels, grain yield was significantly and positively correlated with kernels per spike, kernels per square meter, spikes per square meter and harvest index (Table 4). Grain yield was significantly and negative correlated with plant height. Thousand kernel weight and heading time showed a non significant association with grain yield.

Comparison of the correlation coefficients between agronomic traits in the two levels of N reveals markedly different

Table 4. Correlation coefficients between traits for 24 wheat cultivars grown in high N-level (above diagonal) and low N-level (below diagonal) during 2005–2008

	Grain yield	1000-kernel weight	Kernels per spike	Kernel per square meter	Spike per square meter	Plant height	Harvest index	Heading time
Grain yield	–	–0.234	0.960**	0.967**	0.861**	–0.837**	0.928**	0.363
1000-kernel weight	0.220	–	–0.432*	–0.472*	–0.440*	0.229	–0.224	0.183
Kernels per spike	0.938**	–0.080	–	0.983**	0.803**	–0.795**	0.892**	–0.405*
Kernel per square meter	0.946**	–0.098	0.985**	–	0.897**	–0.807**	0.901**	–0.372
Spike per square meter	0.653**	–0.192	0.601**	0.726**	–	–0.781**	0.811**	0.292
Plant height	–0.687**	0.147	–0.777*	–0.747**	–0.424*	–	–0.787**	0.447*
Harvest index	0.871**	0.000	0.874**	0.890**	0.674**	–0.808**	–	–0.501*
Heading time	–0.329	0.262	–0.391	–0.425*	–0.448*	0.522**	–0.492*	–

Level of statistical significance: * P < 0.05; ** P < 0.01; and ns: not significant.

patterns of response (Table 4). At high N level 1000-kernel weight had significant and negative correlation with all other yield components, while at low N rate no correlations were found between any analyzed traits.

Discussion

These results demonstrated that the grain yield potential of wheat has risen from 4.86 to 7.81 t ha^{-1}. The average rate of grain yield increase per year for the period 1955–2006, estimated for the slope of the linear regression graph, was 41 kg ha^{-1} (0.62%) per year of release. This is in agreement with the findings of Brancourt-Hulmel *et al.* (2003), Donmez *et al.* (2001), Guarda *et al.* (2004), Slafer and Andrade (1989) which have shown an increase in yield potential of Argentinean, US, French and Italian winter wheat cultivars over years of release. An increased emphasis on selection for yield per se coupled with the evaluation of new sources of potential germplasm seem to have been the key factors for the progress obtained in grain yield potential (Borojevic 1990, Calderini and Reynolds 2000, Reynolds *et al.* 2009). For example, the improvement of kernels per spike can be attributed in part to the effect of the dwarfing genes coming from Akakomugi and introduced in modern genotypes (Borojevic and Borojevic 2005a). These genes have been reported to modify morphogenetic patterns within spikes, which can result in more kernels per spike (Austin *et al.* 1980, Donmez *et al.* 2001, Mladenov *et al.* 2007, Sayre *et al.* 1997). In our study, 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 (–0.48 cm per year), thereby enhancing resistance to lodging. On the other hand, higher spike fertility and improved kernels per spike (0.15 kernel per year) resulted in a rise of kernels per square meter (109 kernel per square meter per year) and of harvest index (0.25% per year).

Thousand kernel weight ranged from 38.0 to 42.4 g without a significant trend with respect to the year of cultivar releasing (slope not significant; Table 2). Perhaps, our data suggest that the higher 1000-kernel weight at low N-level (40.8 g) can be used to improve the lower 1000-kernel weight at high N-level (39.7 g). However, the low 1000-kernel weight at higher N-level was compensated by an increase in spikes per square meter and kernels per spike (Tables 2, 3). Thus, it might be difficult to utilize the higher 1000-kernel weight potential at low N-level without adversely affecting other yield components.

Plant height decreased dramatically passing from 129 cm of cv. Banatka selected from landraces to 83 cm of modern cv. Pesma. In meantime, plant height of the cultivars released after 1970 were significantly lower than the earlier ones. Remarkable reduction of height was attained in Sava (89 cm) and Zlatna dolina (84 cm) with the introduction of the wheat dwarfing (*Rht*) genes. More recent cultivars were taller than Zlatna dolina, suggesting that the yield potential increase after 1970 was not associated with reduced plant height. Under conditions of Serbia, during this period, the breeding activities were towards yield improvement, which brought together the plant height trait. The modern cultivars carrying the dwarfing genes recorded plant height around 90 cm. But, most current leading cultivars in the world collection have plant heights around 75 to 85 cm, suggesting that combination of *Rht-B1b* or *Rht-D1b* with *Rht 8* confer optimal plant height for this region. Mean plant height of wheat cultivars represented in this study was 93 cm at low N and 99 cm at high N. On both N-levels, tall cultivars were relatively similar in plant height, between themselves. But on the other side difference between underneath cultivars was higher.

The significant reduction in plant height and increase in harvest index in Serbian wheat cultivars are in agreement with other reports (Brancourt-Hulmel *et al.* 2003, Cox *et al.* 1988, Zhou *et al.* 2007). Harvest index, which represent the capacity to partition dry mater into grain, varied from 0.294 to 0.482 (Table 3). Higher yields may be obtained by increasing total dry matter production, harvest index, or both. In our results, grain yields have been increased mainly due to increased harvest index. Since the theoretical upper limit for the harvest index was established by Austin *et al.* (1980) in ca. 62% under non-stressed conditions, and being the harvest index of modern cultivars in our experiments near 47%, it seems that this trait could be further increased. Nevertheless, the highest harvest index achieved in this study (49,8%, at high N) was similar to the highest index corresponding to US, French and Italian modern cultivars (Brancourt-Hulmel *et al.* 2003, Donmez *et al.* 2001, Guarda *et al.* 2004). Thus, the above-mentioned theoretical upper limit could be inappropriate for semiarid conditions. But, genetic improvement in wheat yield has often been accompanied by a reduction in straw yield with little or no change in total dry matter production (Austin *et al.* 1980, Brancourt-Hulmel *et al.* 2003, Donmez *et al.* 2001). Since the increases in grain yield that are obtained via improved partitioning of dry matter to the grain (i.e. harvest index) must eventually reach a plateau (Austin *et al.* 1980), it has been suggested that further yield improvement will only be achieved if total dry matter is increased without losses in the current harvest index levels (Borojevic 1990, Donmez *et al.* 2001, Feil 1992).

An increase of yield has been reported in all countries practicing intensive wheat breeding, with an annual rise of about 1% (Brancourt-Hulmel *et al.* 2003, Cox *et al.* 1988, Sayre *et al.* 1997, Zhou *et al.* 2007). In our study, the increase of yield resulting from breeding was accompanied by a decrease of plant height and an increase in kernels per spike and spikes per square meter. The reduction of plant height was pronounced during the initial stages of the breeding effort, when dwarfing genes (*Rht*) were incorporated into new cultivars (Sava, Zlatna dolina). This incorporation reduced plant height by about 25 cm relative to Bezostaja 1. In the subsequent phases of the domestic wheat breeding effort, the consensus remained that the optimal plant height for the conditions of southeastern Europe was 80–90 cm (Borojević

1990, Misic and Mladenov 1998). The increase of yield and the reduction of plant height were accompanied by changes in other wheat traits as well (Brancourt-Hulmel *et al.* 2003, Feil 1992, Reynolds *et al.* 2009). In the present study, despite the fact that significant differences in 1000-kernel weight were observed among the cultivars, no increase of this trait has been found to have occurred. This leads to the conclusion that the increase of yield has mostly been a product of increased kernels per spike. The decrease of plant height led to the redistribution of nutrients in favor of the spike, which resulted in an increase of the harvest index and hence an increase of yield (Austin *et al.* 1980). However, the increased productivity of the new cultivars cannot be attributed exclusively to organic matter redistribution due to the indirect effects of *Rht* genes, since the effects of separate genes for kernel number and weight per plant contributed to the increase as well (Dencic 1994). The kernel number increased because of the increased number of flowers, while nutrient redistribution in favor of the spike fostered more successful pollination and normal embryo development, resulting in an increased number of kernels per spike.

Nitrogen application is an important input for winter wheat production. Increasing levels of N fertilizer usually improve grain yield. Generalized responses of the wheat crop to increased N rates are a higher tiller density, higher ear density, more grains per ear, and a reduced 1000-kernel weight (Varga *et al.* 2001). A level of N × cultivar interaction was found for grain yield and all yield components, plant height, harvest index and heading time, which indicated that cultivars responded differently under various production input level. The level of N × cultivar interaction could be explained partly due to the superiority of the modern cultivars, as these are generally more suitable and responsive to increased N input than were their predecessors, and partly as consequence of their decreased plant height, i.e. greater lodging resistance. The average yield increase with the low N compared with the high N treatment for Cipovka (a high-responsive cultivar) and Bankuty 1205 (a low-responsive cultivar) was 1.13 (15.6%) and 0.06 t ha^{-1} (1.2%), respectively (Table 2). Spikes per square meter and kernels per spike were determined by N level, because the low N input (65 kg ha^{-1}) during tillering caused a decrease of these traits. Therefore, all cultivars had the greatest decrease in kernels per spike (4.4%) and spikes per square meter (7.8%), leading to the decrease of grain yield (8.6%) at the low N-level (6.26 t ha^{-1}) compared with the high N-level (6.80 t ha^{-1}). A significant reduction of kernels per square meter (12.6%) at lower level of N and its influence on yield was compensated with higher 1000-kernel weight at lower N.

Modern cultivars used N more efficiently then the older ones. According to Moll *et al.* (1982) one of the N use efficiency component is plant ability for N conversion to grain by shoots (utilization efficiency), which could be further subdivided into harvest index and biomass production efficiency (Ortiz-Monasterio *et al.* 1997). In our study, both of the plant height and harvest index were improved by the progressive wheat breeding, which is in agreement with findings by Ortiz-Monasterio *et al.* (1997). They emphasized that progress in improved utilization efficiency is explained by changes in harvest index rather than in biomass production efficiency. However, Brancourt-Hulmel *et al.* (2003) reported that the reduction in height during the second half of the 20th century was not associated with a decrease in biomass production. Barraclough *et al.* (2010) suggested that the greater yield potential of short-straw compared with long-straw cultivars has been achieved by partitioning more dry matter to grain at the expense of straw (a higher harvest index) and not by greater total dry matter production, more N-uptake, or better photosynthesis. Moreover, this yield potential can be fully realized at high N-rates as short-straw cultivars are less prone to lodging. Short-straw cultivars have more grains per ear giving greater yield for the same total N-uptake and total dry matter production. There is evidence that increased dry matter production has contributed to recent gains in yield potential of short-straw cultivars (Foulkes *et al.* 2007).

A cultivar × year interaction for grain yield and other traits (except kernels per spike and harvest index) indicated that environmental conditions also had a substantial influence on cultivar performance. The absence of a year × level of N × cultivar interaction for grain yield in this study suggested differential cultivar sensitivity to stressed growing conditions regardless of the production input levels. The significant contribution of cultivar/environment interaction (C × N and C × Y) to total variability confirms the fact that grain yield is a complex character that depends on a number of traits. The individual contribution of each of these traits may vary in different genotypes and different environmental conditions. For example (in our study), cv. NS 40S could produce many spikes and kernels per spike at high N, more than the all other cultivars, while cvs. Ljiljana and Dragana produce many spikes and 1000-kernels weight at low N. Simonida was intermediate in most values. Effective selection for a particular trait, therefore, requires that agro ecological conditions are identified in which the trait will be expressed to a greater or lesser extent. Moisture and temperature in the region are most often favorable for vegetative growth of wheat during autumn and early spring. Most of the yield components such as kernels per spike are determined during early vegetative stages. However, 1000-kernel weight is determined during late spring and early summer, when drought and heat stresses are more common in the region. Wheat cultivars grown under typical high temperature suffered a mean 6% loss in kernel number but a mean 21% decline in kernel weight (Al-Khatib and Paulsen 1990). The main characteristic of the climate of southeastern Europe is a permanent precipitation deficit, as approximately 5% growing seasons have enough rain at the right time (Mladenov and Przulj 1999). In such conditions, wheat breeding should focus on those yield components that form earlier in the ontogenetic development, such as spikelet number and flower number per spike.

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