Genetic Gain and Traits Plasticity in Wheat Cultivars Developed for Irrigated Ecosystems of NWPZ of India From 1900 to 2016

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Abstract

Knowledge about the yield gain over the years due to associated changes in the yield component traits is essential for a critical understanding of yield-limiting factors. To estimate genetic gain in grain yield of wheat varieties released between 1900 and 2016 for North-Western Plain Zone of India and to identify agronomic and/or genetic basis of the realized gains, two sets of wheat genotypes with 14 and 10 varieties in each comprising mega varieties and two recently developed genotypes were evaluated, under timely sown tilled and early sown conservation agriculture conditions respectively for 4 consecutive years. The average annual genetic gain in grain yield since 1905 under timely sown condition was found to be 0.544% yr\(^{-1}\) over the average of all varieties and 0.822% yr\(^{-1}\) (24.27 kg ha\(^{-1}\) yr\(^{-1}\)) over the first released variety, NP4. The realised mean yield increased from 2950 kg ha\(^{-1}\) of the variety NP 4 released in 1905 to 5649 kg ha\(^{-1}\) of HD 3086 released in 2014. Linear regression analysis revealed a linear reduction in height and peduncle length over the breeding periods with a linear increase in biomass over the years at the rate of 43.9 kg ha\(^{-1}\) yr\(^{-1}\) or relatively at 0.368% yr\(^{-1}\) mainly because of linear increase in days to heading and crop duration. However, it showed no trend for tiller number and thousand kernel weight but an increase of 0.11 grains per spike yr\(^{-1}\) was evident from the study. The absolute and relative gain yr\(^{-1}\) for harvest index (HI) was found to be 0.0007% and 0.198%, however, polynomial regression shows hardly any improvement in HI since 1982. Interestingly, genetic gain evaluation under early sown conservation agriculture conditions for four years shows similar relative gain (0.544%) but higher absolute gain (29.28 ha\(^{-1}\) yr\(^{-1}\)). Major mega varieties like Kalyan Sona, HD2009, PBW 343, HD2967 and HD3086, which occupied comparatively larger area proved to be highly plastic and able to respond well to the improvements in the production environment under timely sown conditions.

Introduction

Wheat (\textit{Triticum aestivum} L.), being an important source of energy, protein, vitamins and many other mineral elements, is the most widely grown crop in the world. Global wheat consumption by 2028 is likely to be 834.8 MT\(^1\) and despite impressive growth in global wheat production in the last decade, the goal of meeting the projected demand in the future is still a tough challenge. Further increase in wheat production will be constrained by the competing demand for the land for other purposes, depleting natural resources, degrading soil health and biotic stresses specifically black and yellow rust in Africa and Asia, respectively, tan spot (\textit{Pyrenophora tritici-repentis}) in South America and \textit{Septoria tritici} blotch (STB), under the temperate condition of Europe\(^2,3\). To feed the ever-increasing world population, though at an unequal rate in different parts of the world, the global average productivity of wheat has to be increased at the rate of 1.3% yr\(^{-1}\) to meet demands\(^4\). Stagnating productivity in Europe\(^5\) relatively lower gain in the poor yielding environment's\(^6\), and slowing yield gains in other countries\(^6–9\) are worrying concerns. However in particular, to India, the recent estimates\(^10\) for mega wheat-growing environment in northwestern plains of India is quite assuring. The difference in genetic gain realized across the world can be due to many factors including the available crop growth duration, agronomic practices followed and, prevailing weather and soil conditions. However, breeding improved varieties by nicking various
agronomic and physiological traits have always been the major reason to maximize the genetic gain through per unit area yield increments11–13.

Identification of yield-limiting factors is one of the crucial steps in designing any future breeding strategies. Genetic gains have been largely assessed throughout the world by systematically evaluating the performance of historical varieties released over a century and which dominated the production scenario at different points of breeding time7,14–17. Short term studies limited to a period of the 20th century have reported more than 1% genetic gain per annum for wheat yield18–20 whereas, long term analysis21–23 have reported around 0.5% gain annually. In winter wheat, maximum yield gain (around 1%) have been realized during 1960-200024–26. However, in century-long analysis, the gains were highly tapered27–30. Since the beginning of the 21st century, yield potential progress began to slow down in winter wheat or even reached to plateau in some of the countries31–33 and therefore increased world wheat demand is the most likely to be met by South and East Asian countries including India. A number of these studies have established a fact that the periodic evaluation of released cultivars for associated changes in physiological and agronomic traits, which can thus provide the much-needed cue for future breeding strategies. In China, for example, grain weight and spike weight along with HI and biomass production were found to be the most exploited traits by wheat breeders since mid of 20th century26. In Australia, on the other hand, it was mainly the improvement of HI, responsible for realized yield gain34.

The increased spikes number (@0.30% yr−1) and grains per spike (@ 0.60% yr−1) have brought about the yield gain with no change in grain weight in Spain35. A major jump in yield gain in the past has been realized with the introduction of dwarfing genes, which by reducing the size of vegetative plant organs resulted in better availability of assimilates to reproductive organs and thereby leading to higher yields, which largely came through improved harvest index (HI)25,36. Recent studies, however, are indicating that future gain in yield will come through improved biomass by integrating modern genomic tools and understanding physiological processes2,37 along with structural and agronomic adjustment for lodging resistance2,8,38,39. India has a remarkable run of wheat production since 2011 with some intermittent hiccups due to climatic uncertainty. However, India cannot afford to be complacent on wheat production because of likely increased demand due to an ever-growing population and widening food security net by the Government of India. Wheat being central to food security in India is cultivated throughout the country, however, the northwestern plain zone (NWPZ) with about 11.59 Mha area accounting for 50% of Indian wheat production is the most important environment available in the country. It was, therefore felt necessary to examine the pattern of yield gain through changes in agronomic and physiological traits to formulate future breeding strategies through the identification of important yield-limiting factors. Wheat is a highly popular crop among the farmers in India largely because of certainty in production and the government’s strong minimum support for the purchase. Still, high fluctuation in realized yield among many important states of northern India such as Haryana, Rajasthan, Uttar Pradesh and Bihar40 is frequently observed largely because of a sudden and abrupt rise in temperature towards the terminal growth stage of the crop, management constrains32,41,42 and no time for compensation in short growing varieties particularly under late sown conditions.
Phenotypic plasticity (response of different traits to environmental changes) and an environmental contingent trait expression\textsuperscript{43} have been important adaptive genetic traits and are highly relevant under changing climatic conditions. With no limitation of land in ancient agriculture, the success of agriculture was measured in terms of produce harvested from the quantity of seed sown and therefore, generally resulting in highly competitive plant type with a large sink and profuse tillering\textsuperscript{44}. Restricted availability of agricultural land for crop production has shifted the focus toward communal plant type yielding more per unit of area sown. Beside this tradeoff between different yield contributing traits is the biggest stumbling block for future gain and for maximizing the fitness of genotype for better yield realization, the plasticity of different traits needs to be better understood\textsuperscript{42}.

In this paper, we examine historical mega varieties of NWPZ released and under cultivation over the last century and one and half decades of the current 21\textsuperscript{st} century. Beside trait 	extit{per se} improvement, we were more interested and emphasized in knowing which traits of these varieties made them highly plastic resulting in their large scale adaptation. We have also tried to analyze whether the recent gain in yield was largely through the development of communal or competitive genotype.

**Results**

**Analysis of variance and differences among wheat varieties released in different decades**

Analysis of variance revealed significant differences between environment (year), varieties released in different years and the breeding periods in India for the most of agronomic traits across years under testing for experiment 1. The varieties were highly significant for all the phenological and component traits except number of tillers (Table 2). Similarly, the year or environment were also significant for all the traits except GPS, PL and CL. The variety × year was non-significant for yield, number of tillers and TGW and significant for all other traits. The contribution of breeding period toward the genotypic sum of squares was largest for yield, biomass, PH, PL and CL and quite large for DH, DM and TGW. The breeding period could significantly explain the variation in all the traits except number of tillers. The breeding period × year was significant for biomass, PH, PL and CL. The genotype within period were found significant for DM, TGW, GPS, PH, SPS and CL.

**Differences among cultivars for yield, biomass and HI**

Yield averaged over four years showed consistent improvement since the beginning of the 20\textsuperscript{th} century when the initial variety NP4 was released for cultivation. The BLUPs estimated over four years of replicated grain yield data also indicated the same trend (Fig. 1). The average grain yield of the varieties NP4 (1905) and C591(1936) bred in the breeding period (BP1) 2949 kg ha\textsuperscript{-1} and 3253 kg ha\textsuperscript{-1} respectively and there is a remarkable gain within first breeding period representing pre-green revolution breeding activities. The next gain was brought by the introduction of dwarf wheat varieties like Sonora 64 (3618 kg ha\textsuperscript{-1}) and Kalyan Sona (3650 kg ha\textsuperscript{-1}) representing the second breeding period (BP2) and the gain in grain yield was equal to what we observed from NP 4 to C 591. However, a quantum jump in productivity
potential was brought about by indigenously bred wheat varieties like HD 2009 (4419 kg ha\(^{-1}\)) and WL 711 (4446 kg ha\(^{-1}\)) representing the third breeding period (BP3). In the next decade and during the breeding period (BP4), the variety HD 2329 was released for cultivation, whose average productivity realised in our experiments was 4586 Kg ha\(^{-1}\). This was then replaced by Veery lines like PBW 343 and WH 542 with IBL/IRS translocation with nominal gain in yield representing the next breeding period (BP5). The gain of PBW 343 and WH 542 over HD 2329 was more apparent during 2018-19 when the urea application was increased to 150 kg ha\(^{-1}\). PBW 343 and WH 542 are of comparatively longer duration and their yield gain is probably more reflected in the crop season with the comparatively longer winter season. The sixth breeding period with varieties PBW 550 and DBW 17 were also not able to completely replace the PBW 343 and WH 542. The biggest jump in grain yield was, however, realised through recent mega varieties representing the last breeding period (BP7) comprising HD 2967 and HD 3086 which simultaneously replaced three varieties namely PBW 343, DBW 17 and PBW 550. Across varieties, biomass has ranged between 8766 Kg ha\(^{-1}\) in NP 4 to 14235 kg ha\(^{-1}\) in HDCSW 16 and it has increased linearly over the years at the rate of 43.60 kg ha\(^{-1}\) yr\(^{-1}\).

**Correlation, Principal component and Genotype× Environment analysis**

The Pearson’s correlation coefficients (Fig. 2) between the traits under study indicated a very strong positive correlation of yield with DM and Biomass followed by TGW, DH and GPS. The negative correlation of yield was observed with PL, PH and CL.

The principal component analysis (Fig. 2) indicated the association of variable traits indicating eigenvectors of yield with DM, Biomass and DH with acute angles with each other. The TGW and GPS although have an acute angle of eigenvectors with yield but have an obtuse angle with each other indicating exclusiveness of these traits. The data points of genotypes bred in a given breeding period are largely following the grouping within breeding period however, there are clear mixing of data points during BP5 to BP7 and there is clear separate grouping in the first breeding period that is before the introduction of semidwarf varieties.

The AMMI analysis showed significant genotype, G× E for grain yield (Table 4). The AMMI biplot analysis could differentiate among the environments and the genotypes while in the case of GGE analysis the environment could be differentiated better.

**Regression analysis**

The multiple regression analysis models identified DH, DM, TKW, PH, GPS and biomass as highly significant traits while number of tillers and CL were found nonsignificant. However, keeping the breeding period as variable although explained the larger amount of variance with an R\(^2\) value of 69% had compounded effect through DH, PH, Biomass, EL and number tillers indicating, therefore, neglecting these traits in the model. The stepwise regression analysis (Table 3) suggested to include DM, Biomass, TGW, CL, GPS, PH and EL traits explaining variance to the tune of 65%.
**Phenological traits**

Analysis of regression detected a significant association between phenological stages and year of release. Slopes of DH and DM vs year of release were significantly greater than 0 (Fig 3a and 3b). Association was much stronger between DM vs year of release than with DH. DH and DM has increased linearly since 1905 in Indian wheat cultivars. In the last 100 years mean heading has been delayed at the rate of 0.09 days per year or 0.09 per cent per year and the recent varieties head 4-12 days later than initial variety NP 4. On the other hand, crop duration increased linearly at the rate of 0.010 days per year delaying the maturity by 5-13 days in the recent varieties. Polynomial regression shows a declining trend in both DH and DM after HD 2967, released in 2011. Both of these traits, however, are highly influenced by environment and genotype x year interaction was very strong.

**Yield and its component traits**

Regression analysis showed that year of release accounted for 90 % of the variation in mean gain yield data of varieties released in different years and the increase in yield was linear over the years (Fig. 4d). An absolute genetic gain for grain yield in the last 115 years is around 24.27 kg ha\(^{-1}\). Relative genetic gain has been found around 0.544 % per year (over the average of all varieties) (Fig 5a) and 0.822 % per year if calculated by taking NP4 as a base (Fig 5b). Plant height (Fig. 3c) was also affected by both genotype and year, however, there was no significant genotype × year interaction. PH ranged 79 cm for HD 2329 to 121 cm of C 591 and the linear regression revealed a linear reduction in height with the year (p=0.005), however, the cubical polynomial regression significantly improved the relationship with R\(^2\) value as high as 0.7942.

Results for productive tillers m\(^{-2}\) shows that there has been a continuous linear improvement in spike m\(^{-2}\), however at a very slow pace of 0.46 tillers per year and with comparatively larger standard error (+/-25.78 tillers) (Fig 4a). Similarly, GPS (Fig 4c) also showed a linear increase over years at the rate of 0.112 grains per spike (p=0.037) with the relative gain being 0.245 per cent in the last 115 years. Flowering nodes have no linear relationship, however, polynomial regression shows the flowering nodes first increase and then slight drops. Interestingly TKW (Fig 4b) showed no linear relationship but cubical polynomial significantly improved the relationship between TGW and year of release (p=0.01). In a curvilinear relationship, year of release accounted for 71.3 % of the variation in TGW.

**Biomass and harvest index (HI)**

The relative annual rate of growth for biomass was 0.358%. Like grain yield, biomass production is also not indicating any saturation and the biggest gain (0.737) was realised after 1992 (WH 542). It was interesting to note that, both linear and cubical polynomial showed a significant relationship between biomass (Fig 3d) and year of release. HI has also increased linearly with the year of release from 0.35 in NP 4 and 0.29 in C 591 to 0.41 in WH 542 released in 1992 and since then there is no improvement in HI. The absolute and relative gain per year for HI was found to be 0.0007 and 0.373%.
Genetic gain under the early sown condition

We carried out this experiment with two assumptions, i) that pre-green revolution cultivars in the absence of irrigation condition used to be sown in mid-October under conserved moisture condition and there sowing in November might not give them an environment for their potential expression and, ii) as the duration of the many high yielding varieties have increased over the years, which exposes them to heat stress toward the terminal stage and therefore, might not be able to realise their full yield potential in November seeding. To make the evaluation more competitive, we added C 306, a genotype released for early sown rainfed conditions and replaced HDCSW16 with HDCSW 18, a variety released for early sown conditions. Some of the other varieties like Kalyan Sona, Sonora 64, DBW 17 and WH542 were dropped. The absolute genetic gain realised in the experiment from 1905 till 2016 was 29.28 kg ha\(^{-1}\) yr\(^{-1}\), at least, five kilograms higher than that realised under timely sown condition. However, the relative genetic gain measured over average value was almost similar in both sets of the experiment. The trend for a linear increase in biomass is stronger under early sown conditions (Fig 6d) and seems to be major factors besides the GPS for yield gain (Fig 6b). TKW which was showing a slight increasing trend in timely sown condition clearly shows a declining trend in early sown condition (Fig 6c), mainly because the GPS in the genotype requiring mild vernalisation is strongly increased leading to some compromise in TKW due to inter floret competition. The duration of stem elongation phase under the early sown condition in mild vernalisation requiring genotype is prolonged resulting in a higher GPS. The absolute (Fig 7a) and relative genetic gain (Fig 7b) over the years showed a significant relationship with the grain yield and year of release under early sown conditions.

Trait plasticity and response to competition

On average, border rows yielded 15% more than central rows of the plot largely because of more space availability between two adjacent plots. No trend was observed for the response to competition in the released cultivars for grain yield (Fig 8a). However, among the early cultivars, C 591 was highly competitive and dwarf wheat introduction was highly non-competitive for yield. Comparatively broader leaves in WL 711 and HD CSW 16, earlier canopy cover in PBW 550, compact plant type in HD 2329, more ground cover in WH 542 and DBW 17 was probably providing them with a competitive advantage. In the present experiment, the response to the competition was calculated to assess whether we are moving toward communal genotypes or not (Table 5). Though there is no trend, most of the dwarf varieties are showing comparatively lesser response to competition for grain yield. There is no linear trend for any of the component traits except for biomass and tiller number (Fig 8b, 8c, 8d). Compilation and analysis of information related to the plasticity of various grain yield forming traits can enhance our understanding of why a particular cultivar becomes a mega cultivar. In Indian wheat cultivation history, probably four real mega cultivars can be defined during the different period and these are Kalyan Sona in the 70s, HD 2329 in the 80s, PBW 343 in 1990s and now HD 2967 and HD 3086 in the second decade of 21st century. All these cultivars except HD 2329 have comparatively higher grain yield plasticity and this has come from different traits in different cultivars i.e. from biomass, tiller number and grain number in Kalyan Sona, from Kernel weight and kernel number in PBW 343 and kernel number per spike in HD 2967 (Table
6). Overall, important varieties like Kalyan Sona, HD 2009, HD 2967, HD 3086 and PBW 343 which occupied comparatively larger area among the mega varieties are highly plastic and able to respond well to the improvement in the production environment.

**Discussion**

In this study, a historical set of bread wheat cultivars released for NWPZ of India were used to investigate the genetic gain, response to competition and trait plasticity for grain yield and component traits. Analysis of variance revealed significant differences between varieties released in different years and the environment for yield and component traits. Earlier studies have also validated that the differences between breeding periods were significant for yield, GPS and TKW, but not for the number of spikes $m^{-2}$ \(^{16,53}\). Having each breeding period represented by at least one genotype; variance analysis revealed little or no differences among the genotypes within each breeding period for yield, biomass, DM and even PH. Genotypes within the breeding period were differing for DH in all years under study indicating that no single phenological criterion was adopted by the breeders for developing varieties in a specific breeding period.

It is common perception among the breeders of the current era that yield gain in wheat started with the introduction of dwarf varieties in 1964-66, however, the yield of C 591 over NP4 defies this assumption and shows a remarkable gain within the first breeding period, representing the potential impact of pre-green revolution breeding activities. Current analysis shows that next quantum jump in productivity potential was brought about by first generation products released for cultivation (WL 711 and HD 2329) of indigenous breeding activities involving dwarf introduction. The variety HD 2329 dominated the Indian wheat production scenario for almost 10-15 years in the NWPZ and the researchers started to discuss yield fatigue in rice-wheat cropping system. This jinx was subsequently broken by the release of Veery lines like PBW 343 and WH 542 with IB/IR translocation. Farmers in two major states of NWPZ, amplified the realised gain by seeding PBW 343 slightly early because of its mild vernalisation requirement and using slightly higher dose of nitrogenous fertilizer. The response of these varieties to higher dose of nitrogenous fertilizer was also distinctly visible in our results too. PBW 343 comprising Yr 23 and Yr 9 genes for yellow rust resistance became susceptible to yellow rust pathotype 78S84 and incidence and losses due to yellow rust started building up in first decade of 21st century causing equal concern among farmers and researchers again about the sustainability of rice-wheat cropping system. Subsequent releases like DBW 17 and PBW 550, could not completely replace this varieties. The formal release of HD 2967 in 2011 was a great relief to the farmers and within short span of 3-4 years, it simultaneously replaced PBW 343, PBW 550 and DBW 17. HD 2967 become immensely popular among the farmers with its area crossing over 10M ha in Northern plains and received unprecedented breeder seeds indents of 4000q for the year 2019-20. Yield gain in northern plains was further consolidated by the subsequent release of HD 3086.
In contrast to studies on winter wheat\textsuperscript{31–33} and many other studies on spring wheat\textsuperscript{6-9}, where from beginning of 21\textsuperscript{st} century, yield gain have either started to slow down or even plateaued, we found strong linear increase in wheat yield since 1905 with no indication of yield saturation (Fig. 4d, 5a and 5b). An absolute genetic gain of 24.27 kg ha\textsuperscript{−1} with relative value around 0.544 % per year in century long period is equal or better than many other breeding programmes in the world\textsuperscript{8,15}. Moreover, last decade has seen the strongest yield gain due to better genotypes. To account for the early sown condition vis a vis specifically adapted genotypes favoring higher yield, a separate experiment conducted under early sown CA condition, revealed comparatively higher absolute gain of 29.28 kg ha\textsuperscript{−1} yr\textsuperscript{−1}(6d) but with similar relative value. Similar relative value in both set of condition was because the genotypes with specific adaptation to early seeding due to mild vernalization requirement (C 306, PBW 343, HD 2967 and HDCSW 18) were spreaded across the different breeding period. We carried out this experiment with two assumptions, i) that pre-green revolution cultivars in the absence of irrigation condition used to be sown in mid-October under conserved moisture condition\textsuperscript{2} and there sowing in November might not give them an environment for their potential expression and, ii) as the duration of the many high yielding varieties have increased over the years, which exposes them to heat stress toward the terminal stage and therefore, might not be able to realise their full yield potential in November seeding. To make the evaluation more competitive, we added C 306, a genotype released for early sown rainfed conditions and replaced HDCSW16 with HDCSW 18, a variety released for early sown conditions. Some of the other varieties like Kalyan Sona, Sonora 64, DBW 17 and WH542 were dropped due to their less strong response to early seeding.

Regression analysis clearly indicates DM and DH (Fig 3a and 3b) in Indian wheat varieties has linearly increased over the years significantly. This is in contrast to earlier reports that the yield gain in Mediterranean environment has been due to earlier heading and other study showing no chronological trend\textsuperscript{54}. Analysis of these genotypes for physiological traits like chlorophyll content shows no change or chronological trend and higher capturing of radiation due to increased duration rather than improved radiation use efficiency\textsuperscript{34,55} is the major reason for increased biomass and yield gain. Polynomial regression fitting quadratic function of crop duration vs. year of variety releaseshows a declining trend in both DH and DPM after the release of HD 2967 in 2011. Increased duration, however, introduced instability in production over the years due to sudden rise in temperature toward the terminal stages\textsuperscript{40} and therefore further increase in duration without adjusting the sowing time will be highly unrewarding. Highly significant environment and genotype x year interaction for both of these traits indicate toward the same. The higher realisation of yield gain in early sown experiment was also largely because of longer duration available to genotypes along with simultaneous delay in heading because of optimum combination of vernalisation alleles and being not forced to maturity in adapted genotypes. Less strong linear trend for increased duration and delayed heading in early sown experiment was because of interference of mild vernalisation requirement of certain genotypes and presence of these genotypes in different breeding period. However, still DH accounted for 54 per cent of yield variation in early sown
experiment, interestingly polynomial regression shows no saturation of relationship between delayed DH and higher yield.

Biomass has been one of the most important parameters influenced by wheat breeding activities in India during 20th and 21st century as year of release alone explained 70% (p=0.000178) of biomass variation in the released varieties tested under timely sown condition. Biomass has increased linearly at the rate of 43.60 kg ha\(^{-1}\) yr\(^{-1}\) in century long analysis, however, fractured analysis shows the biggest gain (97.12 kg ha\(^{-1}\) yr\(^{-1}\)) after 1992. As discussed in earlier section, biomass like grain yield increased linearly over the years due to linear increase in duration along with delayed heading. DH explained comparatively more variation in biomass than days to maturity, probably because of conflict introduced by forced maturity in longer duration genotypes (Fig. 9a,b). Quadratic equation fitted for both phenological traits vs biomass, not only improved the level of fitness but also explained almost similar variation.

In contrast to earlier report that biomass has increased due to improved photosynthesis, better stomatal conductance, higher leaf chlorophyll content\(^6\) and improved radiation-use efficiency\(^56\), we found no trend for total leaf chlorophyll content and declining trend for stomata number\(^53\) and increase in biomass has been largely attributed to increased duration with delayed heading (Fig) and to some extent improved higher leaf area index\(^53\). Contribution of biomass toward higher yield realization has earlier been reported by number of studies\(^11,54,34,56,57\) and our study further corroborate that. New cultivars in Indian wheat breeding program have biomass gain parallel to Chinese wheat cultivars\(^11\) (@62.6 kg ha\(^{-1}\) yr\(^{-1}\)). The role of duration in increasing the biomass become more evident in early sown conservation agriculture experiment where the AGG for biomass in the genotype released after 1982 happened @ 175 kg ha\(^{-1}\) yr\(^{-1}\) and per cent variation in biomass explained by DH and DM increased significantly (Fig. 9c,d)

The absolute and relative gain per year for HI was found to be 0.0007 and 0.373% and our results are in contrast to many other studies\(^17,27,58\) showing that yield gain was largely because of the increase in HI with no change in biomass production. Researchers also feel that probably HI has already reached a theoretical limit and a further increase in HI is not feasible\(^59\). Our results are therefore, clearly in agreement with the hypothesis that HI played important role for many years after the green revolution and increased biomass is mainly responsible for yield gain in recent varieties\(^60\). HI in Indian wheat varieties reached a maximum value of 0.419, which is well below the theoretical limit of 0.60 as proposed\(^60\). HI value observed in our experiment under Indian set of condition has shown almost similar increase as in many other countries like around 0.25–0.55 in China\(^11,13\), 0.26–0.42 in Spain\(^22\), 0.21–0.43 in Australia\(^61\). In the most of varieties, trade-off between heavy head and lodging in high biomass wheat crops along with forced maturity due to rise in temperature toward terminal stages generally led poor realization of HI under Indian condition like many other studies\(^8,62\).

Our experiments on genetic gain under early sown conditions with few assumptions showed that the longer DH and DPM were mainly responsible for a big jump in grain yield gain in recent wheat varieties (HD 2967 and HDCSW18) because of their mild vernalisation requirement, however linear regression does
not establish statistically significant trend because of the presence of PBW 343 and C 306 with similar kind of requirement (Fig 6a). TGW showed a declining trend in early sown condition, mainly because the number of grains in the genotype is strongly increased leading to some compromise in grain weight.

Results for productive tillers m$^{-2}$ under timely sown conditions shows that there has been a continuous linear improvement in spike m$^2$, however at a very slow pace of 0.46 tillers per year and with comparatively larger standard error (+/-25.78 tillers) (Fig 4a). Similarly, grains per spike (Fig 4c) also showed a linear increase over years at the rate of 0.112 grains per spike (p=0.037) with the relative gain being 0.245 per cent in the last 115 years. Flowering nodes have no linear relationship, however, polynomial regression shows that flowering nodes first increased and then dropped. Interestingly TKW (Fig 4b) showed no linear relationship but cubical polynomial significantly improved the relationship between grain weight and year of release (p=0.01). In a curvilinear relationship, year of release accounted for 71.3 % of the variation in seed weight. It is interesting to note that trend for yield component traits under early sown CA conditions is not in consistent with timely sown tilled conditions for number of spikes m$^{-2}$ and grain weight, largely because conflict introduced by vernalisation gene and probably role of stem reserve mobilisation under stress induced by rise in temperature toward terminal stage under timely sown condition. Biomass and grain yield potential in wheat is largely set by stem weight and number of tiller produced per unit area$^{63}$ particularly under high yielding environment$^{43}$. No trend in tillering potential under early sowing condition was introduced by inclusion of C 306, a high tillering genotype released in 1965 and HDCSW18, a moderate tillering genotype released in 2016. Strongest component for yield increase under both set of production condition is grains per spike like many other studies$^{57,61,64}$ beside biomass and phenological trait. Grain per spike under early sown condition are showing more strong linear increase than timely sown condition largely because of increased spikelet fertility under early sown condition. The negative correlation between the number of grains per spike and thousand kernel weight suggested as stumbling block$^{34,56}$ for further gain in yield was not apparent in our study as negative correlation was offset by prolonged vegetative phase in recent varieties supporting more number of grains and longer duration providing optimum grain filling period. No of grains per spike has increased linearly because of increase in number of spikelet and floret fertility, though with no change in spike length in contrast to hypothesis proposed$^{66}$. It indicates that both source and sink are at optimum, at least in the recently developed varieties under early sown condition. Declining linear trend for grain weight under early sown condition, however, was mainly because earlier genotypes with lesser fruiting sites and enough reserve were able to fully exploit the available grain capacity to imbibe stem reserve and limitation of individual grain capacity in the recently released variety HD 3086. No strong difference in grain weight under early sown and timely sown condition in one of the recent variety like HD 3086 indicate its limitation about individual grain sink strength. Other probable reason for declining trend for grain weight in early sown condition (Fig 6c) in contrast to timely sown can be due to prolonged stem elongation phase induced by mild vernalisation requirement in some of the genotype resulted into higher number of grains through increased number of spikelets and higher no of florets per node and inter floret competition at each node reduced the grain weight in such genotypes.
Linear increase in peduncle girth under timely sown condition also support our earlier assumption that recent genotypes have probably no limitation of source and increase in biomass beside tiller number is also being contributed by increased stem girth. Similarly, plant height, coleoptile length and peduncle length above flag leaf has declined linearly over the years largely because of dwarfing allele like Rht-B1b, Rht-D1b, Rht-D1c, and Rht8 being used just like other international breeding programme\textsuperscript{66-71} and their associated effect on coleoptile length, peduncle length, and plant height\textsuperscript{72,73} and better resource partitioning. Quadratic equation further improved the relationship ($R^2=0.7942$) and it indicates increasing trend for plant height in the recently released varieties. We, therefore, assume that biggest jump in yield gain achieved in recent years was largely through increase in biomass contributed by increase in height, stem girth and more tillering. Reduction in coleoptile length, however, introduced an uncertainty in crop production because of its unsuitability for deeper seeding in early sown crop under comparatively higher mean temperature\textsuperscript{2} as high temperature depletes the soil moisture quickly in upper profile even under irrigated condition. Generating information on association of other dwarfing gene with agronomically relevant traits like coleoptile length and their utilisation in the breeding programme can resolve these conflicts\textsuperscript{3} as only limited number of dwarfing genes have been exploited in wheat breeding\textsuperscript{74}.

A very strong positive correlation of yield with DM and biomass followed by TKW, DH and grains per spike and, a negative correlation with peduncle length, PH and CL was found. Historical studies have shown that traits such as GPS, biomass, HI, and reduced PH are positively associated with yield\textsuperscript{55,75}. The PCA divided the whole dataset into 10 principal components and the first two principal components together represent only 43.3\% variation indicating the strong importance of traits explained by other principal components. DH, DM, TKW, PH, grains per spike and biomass were identified through the multiple regression analysis models as highly significant traits. Based upon the multiple regression analysis, the traits were selected to establish the relationship between average productivity of the varieties released in NWPZ since 1900 and year of release of the variety.

Under this study, we targeted to evaluate whether yield gain has any association with competitive ability of the genotype as proposed under ideotype breeding concept\textsuperscript{47,76-78} due to impaired detection and response to neighbours along with inability to imbibe the increased available resources\textsuperscript{79,80}. Response to competition was high in the variety C591 and the older tall cultivars provided superior weed suppression and respond well to the availability of space. However, over the years, we found no linear trend in response to competition particularly for yield and biomass, however, the component traits like grains per spike and tiller number shows declining trend. Polynomial regression shows that recent varieties are either neutral phenotype or with slightly higher competitive ability than their immediate predecessor for biomass production and yield. Under changing climatic condition, it is becoming highly important that cultivar should have the plasticity to accommodate environmental variation. It indicates the ability of the genotype to respond for the improvement or deterioration in production environment. Four out of five real mega cultivars, Kalyan Sona, PBW 343, HD 2967 and HD 3086 except HD 2329 showed comparatively higher yield plasticity, which conclusively came from different component traits among these cultivars.
Polynomial regression analysis shows increase in yield plasticity in the recently released varieties comes largely through grain number and seed weight (Fig. 10).

**Conclusion**

The present study establishes the contribution of plant breeding activities carried out in the last 115 years in increasing the wheat productivity in northern plains of India and there is no indication of yield plateauing in near future. The yield gain rate has improved in the last three decades. Yearly gain is robust, linear and equal to the gain achieved in other parts of the world. Under the timely sown condition, which occupies the maximum area, the yield gain came largely through increased crop duration with the delayed heading, higher biomass, HI, improved grain number and tillering with almost negligible contribution from grain weight. An early sown experiment shows nearly 20 per cent higher yield gain per year largely through higher biomass and a greater number of grains per spike. For a developing country like India, where large trained manpower is available, investment in traditional plant breeding can still be highly rewarding. Though the introduction of dwarf wheat leads to gain in productivity, the major gain comes through a subsequent round of breeding involving these varieties and indigenous local strains. Next jump came through Veery derived varieties particularly PBW 343 utilizing mild vernalization requiring genes for higher biomass production. Yield being a function of biomass and its subsequent partitioning to grain, linear increase in HI and biomass is expected. However, our results show that HI during last three decades has remained almost stagnant and yield gain came through improved biomass. Tillers number shows linear increase under timely seeding condition but under early sown, it remained almost unchanged. Among the yield component, grain number make the contribution toward yield improvement both in early sown and timely sown condition. Grain number per spike improved because of a pleiotropic effect of dwarng gene on spike fertility\textsuperscript{81} as well as improved availability of photosynthate to the developing florets resulting in lesser floret abortion and its selection by breeder\textsuperscript{36}. Phenological manipulation, which seems to be saturating under timely sown condition, the trend of latest varieties utilizing mild vernalization genes provide some more scope for yield gain through its manipulation. Modern genotypes are showing either neutral behaviour or a slight increase in response to competition and therefore more an in-depth study is required to understand the role of genotype, resources and non-resource environmental cues in modulating plant-plant interactions and their consequences for plant development and crop yield. Increase in biomass and HI are happening not simultaneously but in separate phase and therefore, with a strong production of biomass in some of the recent varieties, further improvement in HI can lead to next jump in grain yield in wheat. It was also proposed that yield gain can be furthered by crossing complementary genotypes exhibiting high biomass and HI\textsuperscript{82}. We, hereby propose, in the targeted cross, further gain in yield can be realized by fully exploiting the advantage of crop duration by adjusting the time of seeding, exploring the alternate dwarving genes which do not reduce coleoptile length, optimize the biomass production along with structural changes for lodging resistance, increasing the grain weight through optimized spike morphology without compromising grain number and increasing sugar reserve mobilization toward sink in case of sudden rise in temperature toward terminal stage.
Methods

Plant material

The experimental material consists of a set of 14 and 10 bread wheat genotypes comprising mega varieties predominantly grown in NWPZ of India during 20th and start decade of 21st century (i.e. between 1900-2016) along with one variety registered with the protection of plant variety and farmer’s rights authority (PPVFRA) for its suitability to conservation agriculture (CA) condition. The two sets were formed for evaluation under timely sown tilled and early sown CA conditions, respectively. The varieties were chosen as they are assumed to cover the maximum wheat grown area during their period of cultivation except for two recent varieties i.e. HDCSW 16 and HDCSW 18 in NWPZ (a prominent wheat-growing region with more than 50% contribution to countries total wheat production) of India since 1905 till 2016. List of varieties, their pedigree, developing Institute and year of identification/release are detailed in Table 1.

Field Design and Data Collection

The first set of 14 wide adapted bread wheat genotypes were grown during 2012-13, 2013-14, 2016-17 and 2018-19 crop seasons in the experimental farm of Indian Agricultural Research Institute (IARI), New Delhi. During 2012-13 and 2013-14, the material was raised in a randomized block design of two replications in a plot of six rows of 5.0 m length spaced at 0.20m apart with a seeding density of 350-400 seed m⁻². Excluding two border rows, all the data points were collected on only the central four rows, to avoid any border effects. During 2016-17 and 2018-19, the plot size was increased to 12 rows with similar spacing and row length and data was collected on the central ten rows. A uniform population was maintained in each plot by seeding rate equivalent to 100 kg/ha for an approximate 36 g/1000 seed test weight. The soil at the experimental site is alluvial with slightly alkaline characteristics and clay loam texture having low organic matter. The area has a semi-arid, + sub-tropical climate with an average annual rainfall of 700 mm and the crop was irrigated as and when required. Fertilizer dose equivalent to 120 kg of N, 60 kg P₂O₅, 60 kg of K₂O, 25 kg of ZnSO₄ per ha was applied during 2012-13, 2013-14 and 2016-17 whereas, during 2018-19 the dose of nitrogenous fertilizer was increased to 150 Kg ha⁻¹ under conventional tillage. In the second experiment, the dose of fertilizer was the same except for 120 Kg ha⁻¹ during the first two years and 150 Kg ha⁻¹ in the last two years. Half the dose of urea and a full dose of P₂O₅ and K₂O were incorporated in the soil before seeding as basal. The remaining half of urea was applied as a top dressing after the first and second irrigation. To control the incidence of wheat rusts and aphid infestation, a prophylactic spray of a fungicide, propiconazole 25 EC, and pesticide, imidacloprid @ 20g a.i. per ha were done. Weeds infestation was controlled either manually or by application of selective herbicide as per need arisen. As crop lodging has been a more common phenomenon in these years in India, the non-shading net was used to avoid the lodging of the crop under conventionally tilled conditions. Also on assumption that many tall varieties and some of the recently released varieties are adapted to early seeding, a separate experiment with 10 released varieties was carried out during 2015-16, 2016-17, 2017-18 and 2019-20 under conservation agriculture condition by seeding between 15-25th
October. Under the no-till condition, no support was provided with the non-shade net as CA generally supports high biomass without the incidence of lodging even for tall varieties. In the case of the experiment under CA condition, glyphosate was used before seeding of wheat crop to kill all germinated weeds. In all growing seasons, efforts were made to create a non-yield-limiting environment. Both the border rows and remaining four central rows were hand-harvested, threshed, dried and weighed separately to record grain yield as tons ha\(^{-1}\) at a maximum of 12% seed moisture content.

The traits, days to 50% heading (DH), days to physiological maturity (DM), plant height (PH), ear length (EL), no of florets, number of grains per spike (GPS), thousand kernel weight (TKW), peduncle length (PL), coleoptile length (CL), spikelets per spike (SPS) total biomass, and grain yield were measured in different trials. The data on DH and DM were recorded as per Zadocks stage 59 and Zadoks stage 89 respectively, when more than half of the tillers exhibited heads out and the day when more than half of the spikes in a plot showed yellowing\(^45\).

Plant height was recorded at the time of physiological maturity (Zadoks stage) by measuring the length from the base of the plant to the tip of the main spike excluding awns. The number of florets was counted on ten randomly selected spikes as the number of differentiated florets 5-10 days after anthesis. The GPS was counted after harvesting and threshing the ten random spike from each plot at maturity. After harvesting and threshing, a random sample was taken from each plot and 250 grains were counted, dried in an oven at 65\(^0\)C for 48 hrs to measure TKW. The grain yield and plant biomass were measured after harvesting the central four rows and drying in the field for four days with due care to avoid the humidity at night.

Analysis of variance was performed by assuming the effect of varieties, replicate, year, and breeding period as a fixed effect, variables were taken as a random effect and the interactions of varieties with year, breeding period for a particular trait as the mixed effect. The analysis was done using R software\(^46\). Linear, quadratic, and cubical polynomial regression equations were drawn to decipher the effect of date of release by using the mean data over four years in both experiments. Linear equation was used to estimate the absolute or relative gain (%) for yield and its component traits, where, \(y_i\) is the mean value for the cultivar for each variety and \(x_i\) is the year in which variety was released. \(e\) indicates the residual error. Phenotypic plasticity for each trait and variety was quantified by calculating a ratio of the standard deviation of the trait for each variety to the overall phenotypic standard deviation of the population of varieties. Response to competition was calculated as per the procedure mentioned \(^{47,48}\).

The stepwise regression analysis was performed to further identify the key traits responding to yield realization using the backward regression approach by eliminating the least contributing factors. The genotype × environment interaction was estimated and elaborated using AMMI and GGE models. The BLUP based factor analysis interaction was used to identify the pattern of gain in yield in the varieties released during the different breeding period. All the multivariate analysis was done in R software using metan R-package\(^{49,50}\). The correlation and principal component analysis was also performed using R-software using ggcorplot\(^51\) and factoextra\(^52\) packages.
Declarations

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AUTHOR CONTRIBUTIONS

RY and SG conceived the idea, hence equally contributed. All authors contributed in conducting the experiments, analysis and article edits.

COMPETING INTERESTS STATEMENT

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Tables

Due to technical limitations, table 1 is only available as a download in the Supplemental Files section.

Table 2. Analysis of variance for yield and its contributing traits
|                          | Genotype | Year | Genotype × year | Breeding period | Breeding Period × Year | Genotypes within breeding period |
|--------------------------|----------|------|-----------------|-----------------|------------------------|----------------------------------|
| **DF**                   | 13       | 3    | 39              | 6               | 18                     | 7                                |
| **Grain Yield**          |          |      |                 |                 |                        |                                  |
| SS                       | 69322117 | 23685282 | 9451254         | 67895223        | 5091253                | 1426894                          |
| Mean Squares             | 5332471  | 7895094 | 242340          | 11315871        | 282847                 | 203842                           |
| Probability              | < 2e-16  | 1.3e-14 | 0.162           | < 2e-16         | 0.116                  | 0.861                            |
| **Tillers per plant**    |          |      |                 |                 |                        |                                  |
| SS                       | 48911    | 120768 | 133735          | 12152           | 93346                  | 36759                            |
| Mean Squares             | 3762     | 40256 | 3429            | 2025            | 5186                   | 5251                             |
| Probability              | 0.125    | 7.13e-08 | 0.112          | 0.8             | 0.0149 *               | 0.248                            |
| **Days to maturity**     |          |      |                 |                 |                        |                                  |
| SS                       | 2426.8   | 469.6 | 513             | 1528            | 420.9                  | 898.8                            |
| Mean Squares             | 186.68   | 156.53 | 13.15           | 254.67          | 23.38                  | 128.4                            |
| Probability              | < 2e-16  | 3.39e-13 | 6.61e-05      | 5.77e-13        | 0.08                   | 1.30e-09 ***                     |
| **Days to Heading**      |          |      |                 |                 |                        |                                  |
| SS                       | 2108.8   | 2733.2 | 728.8           | 1603.8          | 269.6                  | 505                              |
| Mean Squares             | 162.2    | 911.1 | 18.7            | 267.3           | 15                     | 72.13                            |
| Probability              | < 2e-16  | < 2e-16 | 9.84e-11        | 2.05e-14        | 0.344                  | 0.0691                          |
| **Biomass**              |          |      |                 |                 |                        |                                  |
| SS                       | 159752801| 10848358 | 85849782        | 137888079       | 67569303               | 21864722                         |
| Mean Squares             | 12288677 | 3616119 | 2201276         | 22981347        | 3753850                | 3123532                          |
| Probability              | 9.77e-13 | 0.01310 * | 0.00145        | 6.66e-15        | 6.46e-05               | 0.0547                          |
| **Thousand grain weight**|          |      |                 |                 |                        |                                  |
| Source | SS     | 278    | 219.3  | 1132.8 | 118.4 | 696.9 |
|--------|--------|--------|--------|--------|-------|-------|
|        | Mean Squares |       |        |        |       |       |
|        | 140.75 | 92.67  | 5.62   | 188.8  | 6.58  | 99.56 |
|        | Probability |       |        |        |       |       |
|        | < 2e-16 *** | 1.08e-10 | 0.0567 | 3.96e-12 | 0.921676 | 1.78e-12 *** |

**Grains per spike**

| Source | SS     | 89     | 1443   | 2828   | 699   | 1499  |
|--------|--------|--------|--------|--------|-------|-------|
|        | Mean Squares |       |        |        |       |       |
|        | 332.9  | 29.6   | 37     | 471.4  | 38.8  | 214.1 |
|        | Probability |       |        |        |       |       |
|        | 1.53e-14 *** | 0.2383 | 0.0205 *| 1.74e-09 *** | 0.508 | 1.59e-07 *** |

**Plant height**

| Source | SS     | 398    | 1393   | 10569  | 1072  | 507   |
|--------|--------|--------|--------|--------|-------|-------|
|        | Mean Squares |       |        |        |       |       |
|        | 852    | 132.6  | 35.7   | 1761.5 | 59.6  | 72.5  |
|        | Probability |       |        |        |       |       |
|        | < 2e-16 *** | 0.00107 | 0.04009 *| < 2e-16 *** | 0.00301 | 0.0278* |

**Peduncle length**

| Source | SS     | 10.8   | 609.4  | 1480.6 | 562.9 | 42.8  |
|--------|--------|--------|--------|--------|-------|-------|
|        | Mean Squares |       |        |        |       |       |
|        | 117.19 | 3.6    | 15.62  | 246.77 | 31.27 | 6.12  |
|        | Probability |       |        |        |       |       |
|        | < 2e-16 *** | 0.0777 . | 9.63e-15 *** | <2e-16 *** | <2e-16 *** | 0.548 |

**Number of spikelets**

| Source | SS     | 12.19  | 84.93  | 95.42  | 47.57 | 89.50 |
|--------|--------|--------|--------|--------|-------|-------|
|        | Mean Squares |       |        |        |       |       |
|        | 14.224 | 4.063  | 2.178  | 15.903 | 2.643 | 12.785 |
|        | Probability |       |        |        |       |       |
|        | 3.71e-11 *** | 0.032 * | 0.036 * | 7.92e-06 *** | 0.353 | 4.01e-07 *** |

**Coleoptile length**

| Source | SS     | 0.67   | 10.554 | 8.422  | 8.477 | 1.880 |
|--------|--------|--------|--------|--------|-------|-------|
|        | Mean Squares |       |        |        |       |       |
|        | 0.795  | 0.0224 | 0.2706 | 1.4037 | 0.471 | 0.2686 |
|        | Probability |       |        |        |       |       |
|        | <2e-16 *** | 0.121 | <2e-16 *** | <2e-16 *** | 1.43e-12 *** | 0.0297 * |
Table 3. Summary of stepwise regression analysis without breeding period

| Variable | Method | AIC      | RSS        | Sum Sq    | R-Sq     | Adj. R-Sq |
|----------|--------|----------|------------|-----------|----------|-----------|
| DM       | addition | 1827.468 | 75809361   | 36854977  | 0.32712  | 0.321     |
| Biomass  | addition | 1800.18  | 58365283   | 54299055  | 0.48195  | 0.47245   |
| TGW      | addition | 1790.854 | 52751595   | 59912743  | 0.53178  | 0.51877   |
| CL       | addition | 1777.506 | 45996033   | 66668305  | 0.59174  | 0.57648   |
| GPS      | addition | 1770.993 | 42629715   | 70034623  | 0.62162  | 0.60377   |
| PH       | addition | 1767.407 | 40555427   | 72108911  | 0.64003  | 0.61946   |
| EL       | addition | 1766.076 | 39367268   | 73297070  | 0.65058  | 0.62706   |

Table 4. AMMI analysis for grain yield

| Source    | Df  | Sum Sq  | Mean Sq  | F value | Pr(>F) | Proportion | Accumulated |
|-----------|-----|---------|----------|---------|--------|------------|-------------|
| ENV       | 3   | 23685282| 7895094  | 35.68909| 2.40E-03| -          | -           |
| REP (ENV) | 4   | 884874.7| 221218.7 | 1.23416 | 3.08E-01| -          | -           |
| GEN       | 13  | 69322117| 5332471  | 29.7494 | 1.70E-19| -          | -           |
| GEN:ENV   | 39  | 9451254 | 242339.8 | 1.351993| 1.54E-01| -          | -           |
| PC1       | 15  | 5557786 | 370519.1 | 2.07    | 2.72E-02| 58.8       | 58.8        |
| PC2       | 13  | 2707744 | 208288   | 1.16    | 3.34E-01| 28.6       | 87.5        |
| PC3       | 11  | 1185724 | 107793.1 | 0.6     | 8.20E-01| 12.5       | 100         |
| Residuals | 52  | 9320810 | 179246.4 | -       | -       | -          | -           |
| Total     | 150 | 1.22E+08| 814103.9 | -       | -       | -          | -           |

Table 5: Grain yield and response to competition for yield in cultivars released over the years
| Variety       | Grain Yield (Kg/ha) | Response to competition for yield | Type of genotype |
|---------------|---------------------|-----------------------------------|------------------|
|               |                     | Yield                              | Biomass          |                  |
| NP 4          | 2949.753            | 111.2949                          | 89.41154         | NC               |
| C 591         | 3253.533            | 116.3677                          | 124.3056         | C                |
| SONORA 64     | 3618.616            | 109.0458                          | 85.70714         | NC               |
| KALYAN SONA   | 3650.995            | 99.79846                          | 101.6185         | NC               |
| HD 2009       | 4419.811            | 121.3589                          | 133.5878         | C                |
| WL 711        | 4446.363            | 116.2602                          | 135.835          | C                |
| HD 2329       | 4586.856            | 113.029                           | 134.3564         | C                |
| WH 542        | 4767.799            | 127.4854                          | 114.5005         | C                |
| PBW 343       | 4646.559            | 116.4033                          | 113.1505         | NC               |
| PBW550        | 5116.868            | 123.8471                          | 120.5556         | C                |
| DBW 17        | 4825.611            | 114.7973                          | 126.9841         | C                |
| HD 2967       | 5263.288            | 106.5891                          | 118.9499         | NC               |
| HD 3086       | 5648.943            | 113.8737                          | 116.5461         | NC               |
| HDCSW 16      | 5352.087            | 120.0304                          | 126.2535         | C                |

*NC- Non Competitive, C- Competitive

Table 6: Trait plasticity in the genotypes released over the last 100 years
| Variety      | Release year | Trait plasticity |
|-------------|--------------|------------------|
|              |              | Yield            | 1000 kernel weight | Kernel number | Tillers number |
| NP 4        | 1905         | 0.383026         | 0.478035          | 0.276739      | 1.091124       |
| C 591       | 1934         | 0.60013          | 0.247056          | 0.725794      | 0.922902       |
| Sonora 64   | 1965         | 0.72137          | 0.23232           | 0.457019      | 1.327552       |
| Kalyan Sona | 1967         | 0.965657         | 1.292664          | 1.156357      | 1.240012       |
| HD 2009     | 1975         | 0.743617         | 0.449985          | 0.215656      | 1.113342       |
| WL 711      | 1977         | 0.636134         | 0.725085          | 1.231849      | 0.687181       |
| HD 2329     | 1985         | 0.565496         | 0.988142          | 0.613168      | 0.813527       |
| WH 542      | 1992         | 0.57611          | 0.264158          | 0.516264      | 1.004723       |
| PBW 343     | 1996         | 0.67475          | 0.546696          | 0.619719      | 0.908506       |
| PBW 550     | 2006         | 0.510284         | 0.552944          | 0.674058      | 0.787816       |
| DBW 17      | 2007         | 0.55182          | 0.498022          | 0.582023      | 1.232777       |
| HD 2967     | 2011         | 0.835045         | 0.504635          | 0.740293      | 0.612293       |
| HD 3086     | 2016         | 0.74585          | 0.497173          | 0.922228      | 1.108953       |
| HD CSW 16   | 2014         | 0.507393         | 0.577998          | 0.501025      | 0.775689       |

Figures
Figure 1

The box plot (based on BLUP) of yield over genotypes under timely sown conditions and yield of genotypes from different Breeding Periods.
Figure 2

Correlation Plot with hierarchical clustering of traits and principal component analysis.
Figure 3

Regression equation between phenological traits and yield component traits against the year of release.
Figure 4

Regression equation between yield and its component traits with year of release of wheat cultivars
Figure 5

Relative genetic gain over the average of all varieties and NP4 as a base variety
Figure 6

Regression equation between phenological and yield component traits against year of release under early sown conditions
Figure 7

Absolute and relative genetic gain under early sown conditions
Figure 8

Relative competitiveness for yield and component traits against year of release
Figure 9

Increase in biomass due to increased duration and delayed heading:

- Days to heading vs biomass under timely sown condition
  - Figure 9a
  - Equation: $y = 2.8972x^2 + 872.29x + 87.686 \times 10^5$
  - $R^2 = 0.883$
  - Equation: $y = 263.65 \times 12769$
  - $R^2 = 0.5971$

- Days to maturity vs biomass under timely sown condition
  - Figure 9b
  - Equation: $y = 13.4986x^2 + 5497.1x + 74602\times 10^5$
  - $R^2 = 0.9851$
  - Equation: $y = 225.57 \times 13219$
  - $R^2 = 0.4167$

- Days to heading vs biomass under early seeding
  - Figure 9c
  - Equation: $y = 256.88x + 20683$
  - $R^2 = 0.9226$

- Days to maturity vs biomass under early seeding
  - Figure 9d
  - Equation: $y = 554.18x + 72897$
  - $R^2 = 0.784$

Figure 10

Trait plasticity for grain and its linear relation with grain number in wheat genotypes:

- Plasticity for yield
  - Equation: $y = 0.0001x^2 - 0.0000x + 1.2116 \times 10^2$
  - $R^2 = 0.4318$
  - Equation: $y = 16.06x^3 + 0.0076x^2 + 16.729x + 9724.6$
  - $R^2 = 0.3663$
  - Equation: $y = 0.0011x + 1.4460$
  - $R^2 = 0.0506$

- Grain number vs yield plasticity
  - Equation: $y = -0.0342x^2 + 6.6102x - 3.5463x + 1.2272$
  - $R^2 = 0.4694$
  - Equation: $y = 0.2643 + 0.4634$
  - $R^2 = 0.2618$
Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Table1.JPG