Genetic Progress in 50 Years of Potato Breeding in India: Where Do We Stand?

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Abstract

Although the potato is a crop that was introduced in India, it has become a staple food and is grown in both the hills and plains. Potato breeding started in India in the 1950s' and has contributed significantly to improving production. However, it is important to ascertain genetic progress in terms of changes in its yield over time. This study used the 'Era trial' methodology, wherein 22 potato varieties released in different decades ranging from 1968-2012 were evaluated in replicated multi-location trials for three consecutive years (2014-15, 2015-16 and 2016-17) in four potato growing zones of the country. The traits recorded were total tuber yield, marketable tuber yield and tuber dry matter content. Mixed model REML analysis showed significant differences among varieties and environments. Tuber dry matter content showed the least variation among varieties. The highest tuber yields were observed in the West-Central plains (WCP), while mean tuber yields were high in the North-Western plains (NWP). The zone-wise entry mean based broad-sense heritability estimates for all the three traits were high, although individual environment estimates observed low and moderate heritability too. Genetic gain results showed a positive trend for total and marketable tuber yields in NWP, WCP and Hill region (HR), while no gain was observed in the Eastern plains (EP) zone. The maximum annual rate of genetic gain for total tuber yield was 0.4%, 0.3% and 0.2% in WCP, HR and NWP. Positive genetic gain for tuber dry matter content was 0.2% in HR and 0.08% in WCP, while the other two zones had negative genetic gain for the trait. The annual rate of genetic gain for tuber yields and dry matter in potatoes does not commensurate with the future demand for the crop, underlining the need for holistic modern breeding techniques to boost genetic gains in potato breeding in India.

Keywords: Breeding, Genetic gain, Heritability, India, Potato, Yield potential

Introduction

Potato (*Solanum tuberosum* L.) is the world's third most important food crop after rice and wheat (Jansky and Spooner, 2018). It is grown globally and produces more food per unit area in comparison to major grain crops. Potatoes are a wholesome food crop because of their high yield potential, edible energy and nutritive value. To highlight its value as a global food, the Food and Agriculture Organization of the United Nations declared 2008 as the Year of the Potato. The worldwide demand for the crop has been growing continuously. It was grown on 17.34 million hectares (ha) globally, with a production and productivity of 370.43 million tons (t) and 21.36 tons/ha, respectively in 2019. India is the second-largest producer of potato after China, with an area, production and productivity of 2.17 million ha, 50.2 million t and 23.10 t/ha, respectively (FAOSTAT, 2021).

The potato was introduced in India at the beginning of the seventeenth century. A number of European cultivars were introduced but they failed to make an impact due to different agro-climatic conditions. In India, the crop is grown both in the hills and sub-tropical plains, which led to the setting up of the Central Potato Research Institute (CPRI) and an indigenous breeding programme to develop cultivars suited to different agro-ecologies in the country. CPRI is headquartered at Shimla, Himachal Pradesh, with six regional centers spread across different zones in the country. Besides, the All India Coordinated Research Project on Potato started in 1971 is operational in 25 locations to conduct multi-location testing of advanced potato breeding clones. Potato-growing areas in India have been divided into West-Central plains, North-Western plains, Eastern plains, Plateau region and Hills region.

The potato breeding programme at Shimla was initiated in 1935. In due course of time, hybridization between indigenous adapted cultivars and promising exotic introductions resulted in the development of suitable varieties for the sub-tropical plains. To date, 69 potato varieties have been released by CPRI for cultivation in different zones in the country. Most of them are table-purpose, fresh use varieties as the crop was mainly used as a vegetable initially and remained so until the 1990s. The last 2-3 decades have seen the potato processing sector gain major impetus due to changes in food habits of the new generation, in addition to globalization and technology advancements as well as affordability. Significant progress has been observed in potato productivity since 1950 (Fig. 1). However, being a polyploid, heterozygous clonal crop, its breeding process is laborious and time-consuming. Moreover, genetics is complex due to four chromosome copies rather than two in diploid crops. Trait introgression is difficult in the crop compared to cereal crops as the genetic constitution changes in each cross combination or backcrossing due to the heterozygous nature of the cultivars.

Potato breeding in India has mainly focused on tuber yield improvement, followed by tuber quality traits for use in processing. Phenotypic recurrent selection is practiced across generations to select promising clones as new cultivars. In the last two decades, several potato varieties for table and processing purposes have been released in India. However, one of the oldest varieties, Kufri Jyoti, is still cultivated over large areas due to its wide adaptability and tuber quality.

Plant breeding is a continuous step-by-step process that involves time, labour and huge monetary resources. A wrong step can adversely affect the process and lead to huge financial losses to an organization or country. Hence, it is imperative to monitor the efficiency of breeding programmes in terms of genetic gain for target traits to devise new strategies to develop better cultivars (Streck et al., 2019). Genetic gain can be estimated in two ways, as expected genetic gain and realized genetic gain. The expected genetic gain method is based on the response to selection in a single season calculated using the breeders' equation. Realized genetic gain for a trait or index of traits has been defined as the change in the average breeding or genetic value of a population over at least one cycle of selection, while the change in breeding value over many cycles or years is referred to as genetic trend (Rutkoski, 2019a). Realized genetic gain for a trait can be assessed by regressing the average breeding or total genetic value in the year of origin when the genetic trend is linear.

It is important to ascertain genetic gain over the years in potato breeding to modify the breeding strategy. Modern crop breeding and management practices have resulted in an annual genetic gain of 0.8-1.2% in crop productivity especially for cereals, which is inadequate to keep up with the food demand projected in 2050 (Li et al., 2018). The purpose of this study was to estimate genetic progress in tuber yield and dry matter content in different potato growing zones in the breeding programme of the Indian Council of Agricultural Research-Central Potato Research Institute, India, through multi-location evaluation of varieties released between 1968 and 2012.

Materials and methods

Germplasm and experimental setting: Twenty-two potato varieties released between 1968 and 2012 were included in the study to evaluate in 'Era trials' in four different potato growing zones across the country during three years, i.e. 2014-15, 2015-16 and 2016-17 (Fig. 2). Locations with poor data quality were filtered out during the analysis. Annual zone-wise details of the testing locations and varieties included in the analysis are presented in Table 1. The features of the testing locations are listed in Table 2. The crop was raised in the winter season (October – January) in all the locations of the three plain zones, and in the summers (June – September) in hill locations. A standard package of practices was followed in field preparation and crop management. The varieties were grown in randomized complete block design in each location. The plot length was 3 m across the locations while plot size and the number of replications (2-4) varied by the location, depending on the availability of healthy sprouted tubers for planting. There were a total of 10 trials in the North-Western plains, 16 trials in the West-Central plains, 16 trials in the Eastern plains and 5 trials in the Hill region over the years. To ensure consistency, 90-day crop harvest data on total tuber yield, marketable tuber yield and dry matter were considered for all the statistical analyses.

Observations on yield were recorded on the plot basis and converted into tons per hectare for the analysis.

The oldest and latest varieties included in the study were Kufri Jyoti released in 1968 and Kufri Garima in 2012 for all three plain zones. While in the Hill zone the oldest variety was the same, Kufri Girdhari was the latest variety released in 2008 (Table S1).

Data analysis: Restricted maximum likelihood (REML) analysis was performed considering fixed effects for variety and random effects for the environment, replication within the environment and interaction effect of the environment and variety. The environment is a combined parameter for both location and year effects. Heterogeneity of error variances among environments was modelled using a mixed model and adjusted means for all varieties were estimated through the ASReml-R package (Butler et al., 2018). These adjusted variety means were regressed with the year of release of the variety and realized rate of genetic gain was estimated from the slope of the regression line. The relative gain was assessed as percent increase over base predicted mean.

Mixed model equation:

$$Y_{ijk} = \mu + E_i + L_j + R_k + EL_{ij} + \epsilon_{ijk} ;$$

Where, Y_{ijk} is the observed yield in i^{th} environment, j^{th} line and k^{th} replication, μ is the overall mean, E_i is the random effect of the i^{th} environment, L_j is the fixed effect of the j^{th} line, R_k is the random nested effect of replication within an environment, EL_{ij} is the interaction between the i^{th} environment and the j^{th} line, and ϵ_{ijk} is the random error term. All random effects follow an independent and identically distributed multivariate normal distribution. Two kind of analysis were done where we fitted genotypes as random to calculate broad sense heritability in the first model as suggested by Cullis et al. (2006) and in the second model we fitted genotypes as fixed (Mackay et al., 2011 and Piepho et al., 2014), since fitting genotypes as random for genetic gain underestimates the genetic gain estimate.

Results

Mixed model REML analysis

The mixed model analysis showed significant differences among varieties, environment and environment × varieties for total tuber yield, marketable tuber yield and dry matter content in the North-Western plains, West-Central plains, Eastern plains and Hill region except, for environment x variety interaction for total tuber yield in the Hill region (Table 3). The individual location-wise analysis also showed significant differences among varieties in 10, 10 and 16 locations for total tuber yield, marketable tuber yield and dry matter content, respectively. Year × variety interaction was also significant in 10, 10, 5 locations, while variation due to year was significant in 13, 12 and 4 locations for total tuber yield, marketable tuber yield and dry matter content, respectively (Table S2). The analysis clearly showed that tuber yields and dry matter content are highly influenced by the environment, and the environment contributes largely to the total variation for the traits.

Varietal performance

The least-square means for the varietal performance of all the three traits varied over the years in each zone (Fig. 3). In the North-Western plains, Kufri Garima, Kufri Pushkar and Kufri Khyati were leading varieties for total and marketable tuber yields in 2015, 2016 and 2017, respectively. The mean performance for dry matter also showed differences among varieties, although performance varied across the years (Fig. 3). In the West-Central plains, Kufri Khyati in 2015 and Kufri Pukhraj in 2016 and 2017 showed the highest mean total and marketable tuber yields. Kufri Chipsona-1 and Kufri Surya were promising for dry matter. In the Eastern plains too, Kufri Khyati and Kufri Pukhraj showed superior performance for total and marketable tuber yields during all three years. Kufri Surya was promising for dry matter yield. In the Hill region, Kufri Himalini was superior for total yield, marketable tuber yield and dry matter. The year of development and release of top-performing varieties Kufri Garima (2012), Kufri Khyati (2008), Kufri Pushkar (2005), Kufri Pukhraj (1998), Kufri Himalini (2006), Kufri Chipsona-1 (1998) and Kufri Surya (2006) revealed that all high performing varieties in each zone were the latest, released in the last 20 years, except for Kufri Pukhraj and Kufri Chipsona-1.

Location, zone and year-wise analyses

All the three traits under evaluation showed a wide range of variation in each zone with high standard deviation and coefficient of variation observed in the West-Central plains for total and marketable tuber yields (Table 4). The standard deviation and coefficient of variation for the dry matter were low across the zones. The highest total and marketable tuber yields were recorded in the West-Central plains, followed by the North-Western and Eastern plains. However, mean tuber yields were high in the North-Western plains in comparison to the West-Central plains. Although the Hill region recorded the highest dry matter, the variation among varieties was least in the Eastern plains. Mean dry matter was high in the Eastern plains and West-Central plains. Annual zone-wise depiction of trait values in box plots revealed that the data points were more scattered in the West-Central plains for total and marketable tuber yields during all the evaluation years (Fig. 4). Both the yields were high in the North-Western plains in 2015 and 2017, while the West-Central plains observed higher yields in 2016. The overall trend for tuber yields was the North-Western plains followed by West-Central plains, Eastern plains and Hill region (Fig. 4). Dry matter content was high in the West-Central plains followed by the Eastern plains, the Hill region and the North-Western plains (Fig. 4). Broad sense heritability was very high (>90%) for all the three traits across the zones (Table 4) but location-wise heritability values varied from 33.1-99.2, 22.7-98.8 and 43.7-99.5 for total tuber yield, marketable tuber yield and dry matter content, respectively (Table S3).

Zone and year-wise genetic gain analysis

North-Western plains: The relative genetic gain over the locations and years for total tuber yield was 0.230%, while marketable tuber yield observed a gain of 0.192%. Dry matter content recorded negative genetic gain (-0.070%) in combined analysis over the locations and years (Table 5). The annual genetic gain was 0.08 t/ha and 0.06 t/ha for total tuber yield and marketable tuber yield, respectively. The coefficient of determination (R^2) value was minimum (0.08) for dry matter content and maximum for total tuber yield (0.21), (Table 5; Fig. 5).

West-Central plains: In this zone, evaluation of 13 varieties resulted in 0.404% and 0.308% relative genetic gain for total tuber yield and marketable tuber yield, respectively. Low genetic gain (0.079%) was observed for dry matter content (Table 5). Annual genetic gain for total and marketable tuber yields was 0.08 t/ha and 0.11 t/ha, respectively while the gain for the dry matter was negligible. Again, the least R^2 value was observed for dry matter content (0.03) and the total tuber yield recorded the highest value (0.29) (Table 5; Fig. 5).

Eastern plains: In the Eastern plains, 12 varieties were evaluated. The relative genetic gain for all three traits was nil to negative. The relative genetic gain for total and marketable tuber yields was -0.031% and -0.032%, respectively, while dry matter content observed a negative genetic gain of -0.028%. The value for the slope of regression was -0.01 for all the three traits, indicating no gain in absolute values too (Table 5; Fig. 5).

Hill region: A set of six varieties was evaluated in two Hill locations for genetic gain analysis. The Hill region recorded a low relative genetic gain of 0.302% for total tuber yield and 0.320% for marketable tuber yield. In comparison to Indian plains, the realized genetic gain for dry matter content was positive and moderate (0.214%). The slope of regression which depicts the absolute values for realized genetic gain was however low (Table 5; Fig. 5).

The results of the genetic gain analysis were based on a combined analysis of three years' data. Year-wise genetic gain analysis was also performed to observe the variation over the years. The results were similar with a few exceptions for all the three traits under study (Table S4, Figs. S1-S4).

Discussion

Despite tremendous genetic diversity, only modest gains in pathogen resistance have been achieved in potato breeding globally, while genetic progress has been negligible for tuber yield and quality traits in comparison to major cereals (Jansky and Spooner, 2018). This is mainly due to the potato's complex inheritance, heterozygosity, clonal propagation and the poor use of quantitative genetics. This underlines the need for a change in breeding strategy as well as an assessment of the genetic gains made across regions or target population environments (TPEs). In India, potato is grown in diverse agro-ecologies ranging from the temperate hills to subtropical and tropical plains. These conditions are entirely different from those in major potato-growing areas of Europe and the USA. The Indian breeding programme involves the evaluation of advanced clones in TPEs before releasing them as new varieties. Thus, we considered a zone-wise evaluation of genetic progress in total tuber yield, marketable tuber yield and dry matter content of the Indian potato breeding programme led by ICAR-CPRI.

The North-Western plains have a major area under potato cultivation in India, followed by the Eastern plains, the West-Central plains and the Hills and plateau region (Pradel et al., 2019). In our study, the mixed model analysis for each zone showed statistically significant differences among varieties for all the three traits, with a greater contribution of the environment to the total variance. This suggests high genetic variability among the varieties used in the study. The high contribution of the environment could be attributed to diverse locations under each zone in the analysis. Kufri Khyati and Kufri Pukhraj were found to be the common promising varieties across the zones for total and marketable tuber yields, except in the Hill region. Similar performance of these two varieties in the Indian plains was observed in an earlier study (Sood et al., 2020a). Besides, Kufri Garima and Kufri Pushkar also showed their superiority in the North-Western plains. Nevertheless, Kufri Himalini was the top variety for all the three traits under evaluation in the Hill region. Although the variation for the dry matter was low in comparison to both tuber yields due to the least involvement of varieties suited to processing in the study, Kufri Chipsona-1 and Kufri Surya demonstrated their superiority for dry matter content across the zones and years. These results demonstrate that varieties released in the last two decades, i.e., after 2000, have higher trait performance than varieties released before 2000. The highest tuber yields in the West-Central plains corroborate an earlier study (Pradel et al., 2019) and data on crop yields of the Directorate of Economics and Statistics, Government of India. However, the North-Western plains observed the highest mean tuber yields as majority of potato growing locations and conditions fall in this region (Pradel et al., 2019). Even though broad sense trait heritability values were high in each zone, individual environment-wise heritability values varied from low to high for all three traits. Tuber yield is a complex trait and has low heritability while the dry matter is strongly heritable, but affected by the environment (Slater et al., 2014a). This indicates a greater role of the environment in the expression of all the three traits under study, and subsequently, low genetic progress is expected in the breeding cycles.

The cost associated with the development of new crop varieties is increasing while land and labour resources are dwindling. Therefore it becomes imperative to design product profiles for TPEs based on predicted and realized genetic gains for traits. Periodic assessment of realized genetic gain is carried out to compare breeding strategies and the effectiveness of breeding programmes (Hallauer et al., 2010; Rutkoski, 2019a). The slope of the regression in the 'Era trial' analysis provides the value of realized genetic gain per year in absolute units (Garrick, 2010). Various methods could be used to evaluate realized genetic gain or genetic trends depending on the availability of data (Rutkoski, 2019a&b). In crop breeding programmes, the evaluation of varieties released overtime referred to as 'Era trials', is one of the prominent methods to understand and quantify realized genetic progress or genetic gain (Duvick, 2005; Rutkoski, 2019a&b). Alternatively, historical trials analysis is also a good option. This study used the 'Era trials' methodology involving popular potato varieties released for cultivation in different years in India to assess the genetic progress of potato breeding in India from 1968 to 2012. The base year was 1968 and the base variety was Kufri Jyoti for all four zones for regression analysis. Kufri Jyoti is a widely adapted cultivar still grown in all the major potato-growing areas of the country. The annual average genetic gain based on three years' assessment ranged from -0.03 - 0.40% for total tuber yield, and -0.03 - 0.32% for marketable tuber yield across the zones. It was interesting to note that the genetic gain for dry matter content was highest in the Hill region (0.21%), followed by the West-Central plains (0.08%), while the Eastern-Western plains observed negative values. High dry matter in the Hill region could be attributed to long-day conditions during the crop season in the hills. Overall, the relative genetic gain for all three traits was very low in the past 50 years. This could be due to the crop's complex genetics, repeated use of the same or same pedigree parental lines in breeding. However, the trend analysis (Fig. 1) shows a consistent increase in potato productivity in India over the years, barring the last 20 years when the tremendous increase in production could be ascribed to an increase in the area rather than in productivity (Fig. 1). This indicates that genetic gain in potato breeding was minimal in the last two decades. Among all the four zones, no genetic gain was observed in the Eastern plains for all the three traits, which could be attributed to the lack of suitable varieties and focussed breeding programme for the zone, and the direct deployment of varieties bred for the North-Western plains in the Eastern plains. Low or negative genetic gain for dry matter content in all the major potato growing regions of the country except the Hill region demonstrated that dry matter has not been given due attention in breeding new varieties in the past 2-3 decades. Although the increase in tuber yield was mainly due to new varieties released in the last two decades, the highest annual genetic gain for tuber yields in the West-Central plains might be the outcome of a combination of improved genetics and better crop management strategies in the region (Muralidharan et al., 2019; Kumar et al., 2021). Consistent genetic gain for all the three traits in the Hill region is the result of focussed breeding for late blight resistance and the release of late blight-resistant varieties such as Kufri Himalini and Kufri Girdhari in the last decade.

This is the first study assessing the genetic gain for tuber yields in India, which indicates that efforts have been successful in increasing potato productivity in all the potato growing zones through genetic means, except in the Eastern plains. However, the realized genetic gain for tuber yields is low in comparison to those for cereals and other major crops in India. An annual genetic gain of 5.4% in pearl millet, 3.8% in maize, 2.3% in rice and 2% in wheat have been achieved in the last three decades in India (Yadav et al., 2021). In another study, Kumar et al. (2021) observed an annual genetic gain of 0.87-1.9% under moderate and severe reproductive stage drought stress in rainfed rice in India. Douches et al. (1996) observed that the genetic potential of new potato cultivars was less than those of old cultivars in the USA because of the greater focus on early maturity and processing quality potato cultivars. Slater et al. (2014b) have suggested that the use of best linear unbiased prediction (BLUP) can enhance genetic gains from 8 to 19 t/ha/year for tuber yields in comparison to phenotypic recurrent selection. Later, Slater et al. (2016) also demonstrated the integration of genomic selection, such as the inclusion of genomic data instead of pedigree information in the estimation of breeding values, which revealed substantial improvement in genetic gain for both low and high heritability traits in potatoes in comparison to both phenotypic and pedigree selection. Similar results have been observed using pedigree-based estimated breeding values and SNP markers-based genomic estimated breeding values in potato breeding (Sood et al., 2020b; Sood et al., 2020c). Recently, several studies on genetic gain have been conducted in different crop breeding programmes to assess and monitor their efficacy (Muralidharan et al., 2019; Streck et al., 2019; Rutkoski, 2019a; Li et al., 2018; Woyann et al., 2019; Breseghello et al., 2011; Júnior et al., 2017). Modern technologies based on quantitative genetics, like estimated breeding values, genomic selection, high throughput phenotyping and gene editing may accelerate genetic gains significantly (Prashar et al., 2013; Slater et al., 2016; Sood et al., 2020b&c; Ortiz, 2020). The cumulative gains from all the approaches will ultimately be reflected in tuber yield, quality and other important economic traits in potatoes.

There is a significant gap in the rate of genetic gain for productivity and quality in the Indian potato breeding programme in terms of projections for 2050 (Vision 2050). The estimated domestic demand for food potatoes is 78 million tons, at an annual compound growth rate (ACGR) of 2.34% and 25 million tons for processing quality potatoes at an ACGR of 6% by 2050. This necessitates the adoption, integration and implementation of novel breeding approaches allowing the selection of multiple desirable traits and reducing breeding cycles and the cost of breeding to bridge yield barriers. The catalyst for this is of course national and international networks with unified standards, digitalizing breeding data, integrating genomics and phenotype data, open access terms for the availability of germplasm, infrastructure and informatics tools which could help modernize breeding to develop high-yielding and better quality potato varieties with resilience to stress (Xu et al., 2017; Li et al., 2018; Cobb et al., 2019).

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Author contributions

S.S.: Conceptualization, V.B. and V.K.: Methodology, S.S., R.D. and A.R.: Formal Analysis, S.K.L., R.K. and S.K.: Field trials conduction, V.K.G.: Seed tuber production, S.S., R.D., A.R. and V.M.: Data Curation, S.S.: Writing and Original Draft Preparation, S.S. and A.R.: Review & Editing, R.K.S. and M.K.: Supervision, A.K.S.: Project and Funding Acquisition

Conflicts of interest

The authors declare no conflict of interest

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Table 1: Locations and varieties included in the study.

Potato growing zones	Evaluation year					
	2014-15		2015-16		2016-17	
	Locations	Varieties evaluated	Locations	Varieties evaluated	Locations	Varieties evaluated
NWP	Jalandhar, Hissar, Modipuram and Pantnagar	Kufri Bahar, Kufri Garima, Kufri Gaurav, Kufri Jyoti, Kufri Khyati, Kufri Pukhraj, Kufri Pushkar and Kufri Sadabahar	Hissar, Modipuram and Pantnagar	Kufri Bahar, Kufri Garima, Kufri Gaurav, Kufri Jyoti, Kufri Khyati, Kufri Pukhraj, Kufri Pushkar and Kufri	Hissar, Modipuram and Pantnagar	Kufri Bahar, Kufri Garima, Kufri Gaurav, Kufri Jyoti, Kufri Khyati, Kufri Pukhraj, Kufri Pushkar and Kufri Sadabahar

				Sadabahar		
WCP	Kanpur, Gwalior, Deesa, Chhindwara and Raipur	Kufri Badshah, Kufri Bahar, Kufri Chipsona-1, Kufri Chipsona-3, Kufri Garima, Kufri Jyoti, Kufri Pukhraj, Kufri Pushkar, Kufri Chandramukhi, Kufri Lauvkar, Kufri Gaurav, Kufri Khyati and Kufri Surya	Kanpur, Gwalior, Deesa, Chhindwara and Kota	Kufri Badshah, Kufri Bahar, Kufri Garima, Kufri Jyoti, Kufri Pukhraj, Kufri Pushkar, Kufri Sadabahar, Kufri Chandramukhi, Kufri Lauvkar,	Kanpur, Gwalior, Deesa, Chhindwara, Raipur and Kota	Kufri Badshah, Kufri Bahar, Kufri Garima, Kufri Gaurav, Kufri Jyoti, Kufri Khyati, Kufri Lauvkar, Kufri Pukhraj, Kufri Pushkar and Kufri Surya

				Kufri Gaurav, Kufri Khyati and Kufri Surya		
EP	Faizabad, Patna, Bhubaneswar, Kalyani and Jorhat	Kufri Ashoka, Kufri Garima, Kufri Gaurav, Kufri Giriraj, Kufri Himalini, Kufri Jyoti, Kufri Khyati, Kufri Lalima, Kufri Pukhraj, Kufri Pushkar, Kufri Shailja and Kufri Surya	Faizabad, Patna, Kalyani and Jorhat	Kufri Ashoka, Kufri Garima, Kufri Gaurav, Kufri Giriraj, Kufri Himalini, Kufri Jyoti, Kufri Khyati, Kufri Lalima,	Faizabad, Patna, Bhubaneswar, Kalyani, Jorhat, Dholi and Pashighat	Kufri Ashoka, Kufri Garima, Kufri Gaurav, Kufri Himalini, Kufri Jyoti, Kufri Khyati, Kufri Lalima, Kufri Pukhraj, Kufri Pushkar and Kufri Shailja

				Kufri Pukhraj, Kufri Pushkar, Kufri Shailja and Kufri Surya		
HR	Srinagar and Shillong	Kufri Girdhari, Kufri Himalini, Kufri Kanchan, Kufri Jyoti, Kufri Megha and Kufri Shailja	Srinagar	Kufri Girdhari, Kufri Himalini, Kufri Kanchan, Kufri Jyoti and Kufri Shailja	Srinagar and Shillong	Kufri Girdhari, Kufri Himalini, Kufri Kanchan, Kufri Jyoti, Kufri Megha and Kufri Shailja

NWP= North-Western plains; WCP = West-Central plains; EP= Eastern plains and HR= Hill region.

Table 2. Geographical location and features of the locations/evaluation sites.

Location/Evaluation site	State	Geographical location		Altitude (m)	Average temperature (ºC)		Soil texture	Annual rainfall (mm)	Growing Degree Days (4°C base temp)
		Latitude	Longitude		Min	Max			
Jalandhar	Punjab	31.17°N	75.32°E	228	16.85	31.09	Sandy loam	769	1664.90
Hissar	Haryana	29.10°N	75.46°E	215	17.40	32.88	Sandy loam	429	1913.75
Modipuram	Uttar Pradesh	29.40°N	77.46°E	237	17.83	30.96	Sandy loam	933	1648.85
Pantnagar	Uttarakhand	29.50°N	79.73°E	244	16.90	29.70	Sandy loam	1548	2151.15

Kanpur	Uttar Pradesh	26.29 °N	80.27° E	168.6	12.44	27.10	Sandy loam	820	1646.80
Gwalior	Madhya Pradesh	26.17 °N	78.13° E	211	18.16	33.63	Silty clay loam	900	1529.35
Deesa	Gujarat	24.50 °N	72.13° E	136	19.00	33.90	Sandy loam	936	2138.65
Chhindwara	Madhya Pradesh	22.03 °N	78.56° E	675	13.07	29.47	Clay loam	1150	2125.85
Raipur	Chhattisgarh	21.23 °N	81.41° E	291	21.07	32.51	Clay loam	1145	1998.15
Kota	Rajasthan	25.11 °N	75.54° E	273	20.46	33.08	Clay loam	761	1998.35
Faizabad	Uttar Pradesh	25.55 °N	81.84° E	98	18.66	34.70	Silty clay loam	1050	1763.45
Patna	Bihar	25.58 °N	85.06° E	57	19.60	31.43	Sandy	1205	1754.55

							loam		
Bhubaneswar	Odisha	20.15°N	85.52°E	45	22.30	33.10	Sandy loam	1502	1425.05
Kalyani	West Bengal	22.58°N	88.25°E	9	23.91	33.58	Sandy loam	1167	2151.15
Jorhat	Assam	26.47°N	94.12°E	87	16.10	28.20	Sandy clay loam	2483	1805.75
Dholi	Bihar	25.50°N	85.40°E	53	19.36	30.65	Sandy loam	1180	1754.55
Pashighat	Arunachal Pradesh	28.07°N	95.22°E	152	19.77	26.55	Sandy loam	4428	1769.25
Srinagar	Kashmir	34.08°N	74.79°E	1585	6.70	18.20	Clay loam	830	1036.35
Shillong	Meghala	25.32	91.50°	1800	14.0	20.0	Loa	2850	1458.5

	ya	°N	E		0	0	m		0

Table 3: Zone-wise mixed model REML analysis across locations and years.

	Total tuber yield			Marketable tuber yield			Dry matter content		
Zone	Fixed effect	Random effect		Fixed effect	Random effect		Fixed effect	Random effect	
	Variety	Env	Env* Variety	Variety	Env	Env* Variety	Variety	Env	Env* Variety
NWP	5.35 **	58.96 **	11.02 **	5.21 **	52.78 **	9.46 **	3.33 **	0.66 **	1.15 **
WCP	4.42 **	73.07 **	23.61 **	4.13 **	82.24 **	20 **	5.47 **	1.58 **	0.53 **
EP	4.53 **	40.15 **	4.82 **	4.12 **	58.07 **	4.28 **	5.57 **	1.72 **	0.39 **
HR	80.82 **	40.75 **	0.03 NS	24.5 **	31.5 **	0.44 **	66.55 **	2.87 **	0.03 *

Note: Env represents environment, which is a combined parameter for both location and year effect.

NWP = North-Western plains; WCP= West-Central plains; EP= Eastern plains and HR = Hill region.

**, * effect is significant at 1% and 5% level of significance, respectively.

Table 4. Basic statistics and trait heritability over locations and years.

Trait	**Zone**	**No of Obs.**	**Min**	**Max**	**Mean**	**SD**	**CV (%)**	**h^2_{bs} (%)**	**1st Quadrant**	**3rd Quadrant**	**Median**
TTY	NWP	236	19.6	58.3	35.8	8.0	6.46	95.7	29.6	41.4	34.9
	WCP	532	13.2	72.1	32.9	10.6	14.55	94.1	25.7	37.5	30.9
	EP	482	12.6	45.5	27.5	6.5	7.13	93.2	22.2	31.9	27.0
	HR	104	10.1	33.4	24.1	4.9	6.25	99.7	18.9	28.9	26.4
MTY	NWP	236	18.6	55.5	32.4	7.3	6.84	95.6	26.8	37.4	30.9
	WC	532	9.4	69.6	28.9	10.	15.89	93.2	22.5	33.3	26.7

	P					7					
	EP	470	8.3	43.7	24.4	7.2	7.99	92.4	18.3	29.7	24.7
	HR	104	7.2	29.1	20.4	4.6	7.58	99.4	16.5	24.4	22.1
DM	NWP	184	12.0	20.6	16.2	1.6	5.02	91.5	15.0	17.2	16.2
	WCP	420	11.5	22.6	18.4	1.6	5.15	96.8	17.3	19.5	18.2
	EP	234	15.5	22.3	18.6	1.3	3.54	97.1	17.5	19.7	18.5
	HR	104	10.9	23.4	16.6	1.8	6.27	99.1	15.1	18.2	16.9

TTY = total tuber yield; MTY = marketable tuber yield; DM= dry matter; NWP = North-Western plains; WCP= West-Central plains; EP= Eastern plains and HR = Hill region.

Table 5: Genetic gain for total tuber yield, marketable tuber yield and dry matter content assessed in Era trials over the locations and years.

Zone	Trait	Intercept	Slope	R^2 (UnAdj)	Base predicted mean	Relative genetic gain
NWP	Total tuber yield	-123.71	0.08	0.21	35.11	0.230
WCP		-196.68	0.11	0.29	28.26	0.404

EP		43.78	-0.01	0.01	27.05	-0.031
HR		-107.04	0.07	0.29	21.67	0.302
NWP	Marketable tuber yield	-90.48	0.06	0.15	32.52	0.192
WCP		-127.89	0.08	0.14	25.23	0.308
EP		38.42	-0.01	0.01	23.66	-0.032
HR		-97.85	0.06	0.23	18.46	0.320
NWP	Dry matter	39.52	-0.01	0.08	16.69	-0.070
WCP		-10.45	0.01	0.03	18.68	0.079
EP		29.52	-0.01	0.01	19.09	-0.028
HR		-49.53	0.03	0.25	15.42	0.214

Figure legends

Figure 1: Trends in area, production and productivity of potatoes in India from 1961 to 2019. (Source: FAOSTAT, 2021)

Figure 2: The zones and locations included in the analysis.

Figure 3: Zone-wise performance of traits of varieties in different years.

[TTY = Total tuber yield (t/ha); MTY = Marketable tuber yield (t/ha) and DM = Dry matter (%)].

Figure 4: Annual zone-wise least-square means for different traits: (a) Tyield = Total tuber yield; (b) Myield = Marketable tuber yield and (c) DM = Dry matter.

Figure 5: Regression plots of realized genetic gain for different traits over the locations and years in different zones of the country

[WCP = West-Central plains zone; EP = Eastern plains zone; HR = Hill region; NWP = North-Western plains zone]

Supplementary material

Table S1: Year of the release of varieties and yearly LS means for three traits.

Table S2: Location-wise mixed model REML analysis.

Table S3: Location-wise basic statistics summary for tuber yield and dry matter over the years.

Table S4: Year-wise genetic gain for total tuber yield, marketable tuber yield and dry matter content assessed in Era trials.

Fig S1: Regression plots of realized genetic gain for different traits in North-Western plains zone.

Fig S2 Regression plots of realized genetic gain for different traits in the West-Central plains zone.

Fig S3 Regression plots of realized genetic gain for different traits in Eastern plains zone.

Fig S4 Regression plots of realized genetic gain for different traits in the Hill region.