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REVIEW ARTICLE

An overview of maize landraces of the North-Eastern Himalayan region of India with special reference to '*Sikkim Primitive*' - a unique landrace with extraordinary prolificacy

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Abstract

Maize landraces serve as a goldmine for novel genes pertaining to tolerance to biotic and abiotic stresses, adaptability, and nutritional quality traits. Worldwide, maize landraces are cultivated in specific areas for their unique characteristics, as preferred by the farming community. In India, the North-Eastern Himalayan (NEH) region is rich in diverse maize landraces, some of which are unique globally. However, the utilization of these maize landraces in breeding programmes has been limited. Here, we discussed the importance of maize landraces as a source of diverse traits, besides mentioning some of the most promising landraces available globally. We presented the extent of genetic diversity present in NEH-based maize landraces using morphological, cytological, biochemical, and molecular markers. The distinctiveness of *Sikkim Primitive* – a unique landrace for its extraordinary prolificacy has been mentioned in detail. We also mentioned the genetic and genomic analysis undertaken on *Sikkim Primitive* for dissecting prolificacy in maize.

Keywords: Corn, population, breeding, genetic improvement, farmers' variety, locals

Introduction

Maize serves as a vital crop for food, feed, fodder, and fuel, along with its extensive industrial applications (Hossain et al. 2023; Tarekegne et al. 2024; Mishra et al. 2025). Taxonomically, maize (*Zea mays* ssp. *mays*) belongs to the Poaceae family and the Maydae tribe (Doebley 2004). It has a somatic chromosome number of 20, a genome size of 2.3 gigabases, and encodes over 32,000 genes (Schnable et al. 2009). The domestication of maize traces back approximately 9,000 years to teosinte grass (*Z. mays* ssp. *parviglumis*) found abundantly around the Balsas River Basin in southwestern Mexico (Matsuoka et al. 2002). Subsequent hybridization with *Z. mays* ssp. *mexicana* in the central Mexican highlands, about 4,000 years post-domestication, further shaped modern maize genetics (Yang et al. 2023). As a result, contemporary maize represents a genetic amalgamation of both *parviglumis* and *mexicana* genomes. Modern maize now possesses unique characteristics suitable for higher grain yield and adaptability to climate change, besides higher nutritional qualities (Hossain et al. 2019).

The molecular basis of maize domestication was explored by Doebley et al. (1990), who identified key genes responsible for its morphological evolution from teosinte. Specific loci instrumental in this transformation include *teosinte branched1* (*tb1*) (Studer et al. 2011; Dong et al. 2019), *teosinte glume architecture1* (*tga1*) (Doebley 2004; Wang et al. 2005; Wang et al. 2015; Studer et al. 2017), *grassy tillers1* (*gt1*) (Whipple et al. 2011; Wills et al. 2013; Wang et al. 2023), *upper plant architecture1* (*upa1*) (Tian et al. 2019), *upper plant architecture2* (*upa2*) (Tian et al. 2019), and *tassel replace upper*

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ears1 (*tru1*) (Dong et al. 2017). These genetic factors played a crucial role in converting wild grasses into cultivated maize (Hossain et al. 2016).

Following its initial domestication, maize diversified in Mexico's highlands, where selection processes led to the emergence of numerous distinct races adapted to different environments (Merrill et al. 2009). Genetic mechanisms, including mutation, migration, and genetic drift, drove this diversification. Over thousands of years, maize spread across the Americas and was introduced to Europe following Christopher Columbus's arrival in the New World on October 12, 1492 (Mir et al. 2013). Through trade and colonization, maize further expanded to Asia and Africa, likely within a century (Prasanna and Sharma 2005). Even today, landraces of South American origin persist in regions such as Italy and Spain. In Brazil, maize landraces emerged from the crossing of varieties introduced from the United States with those cultivated by indigenous communities and European settlers after the discovery of the Americas (Paterniani et al. 2000).

The advent of hybrid breeding, particularly single-cross hybrids, significantly enhanced maize yield potential. However, challenges posed by climate change and a growing global population necessitate the development of high-yielding, nutritionally enriched, and climate-resilient maize hybrids. Despite the vast genetic diversity within maize germplasm, only a small fraction has been utilized in crop improvement programs worldwide. Maize landraces remain an invaluable genetic reservoir, offering novel genes that can contribute to future breeding efforts for sustainable maize production.

Landraces: A foundation for modern maize

Landraces refer to locally adapted varieties of domesticated crops that continue to be cultivated by rural communities through traditional agricultural practices, without the use of formal breeding programs (Monroy-Sais et al. 2024). These landraces are known by various names, including heirloom, ancient, traditional, farmer, creole, folk, and local varieties (Villa et al. 2005). Additional terms used to describe related maize landraces include maize race, ecotype, and native maize variety (Elisa et al. 2022). The long-standing tradition of saving seeds from local maize for food and ceremonial purposes has facilitated the development of diverse subgroups and open-pollinated varieties (OPVs) in the Americas (Xolocotzi, 1985; Samayoa et al. 2018). Unlike hybrid maize, landraces are genetically diverse and heterogeneous, consisting of multiple genotypes selected by farmers for specific traits such as resistance to environmental stresses, flowering time, ear characteristics, plant structure, prolificacy, flavor, and other desirable attributes (Guzzon et al. 2021).

Maize landraces are broadly classified into two categories: the old landraces found in Central and South America (the New World) and the newer landraces that have been cultivated globally (Van Heerwaarden et al., 2011). Before the widespread adoption of hybrid maize, these newer landraces retained substantial genetic diversity (Hong et al. 2024). Local farmers often named landraces based on distinctive features such as ear shape, grain texture, color, plant structure, vegetative cycle, or intended use (Burt et al. 2019). Some well-known examples of such names include White Palamo, Elote Conico, Purple-Pink Xuxuyul, Yellow Conico, White Cacahuacintle and Red Ladrillo (Elisa et al. 2022). Globally, significant maize landraces include Northern Flints, Southern Dents and Corn Belt Dents from the United States; Tuxpeño, Celaya, Chapalote, Olotillo, Serrano, Jala, and Cacahuacintle from Mexico; Cuban Flint from Cuba; Coastal Tropical Flint/Costeño and Tusón/Puya from the Caribbean and northern South America; Cateto and Cristal from Brazil and Argentina; Kenyan Yellow from Africa; Peruvian Purple from Peru; Nepalese Hill Maize from Nepal; Hopi Blue Corn from North America; Italian Eight-Row Flint from Italy; and Sikkim Primitive and Gurez from India. The genetic background of many modern maize hybrids traces back to landraces such as Corn Belt Dents, Northern Flints and Southern Dents (Goodman and Brown 1988; Troyer 1999).

Landraces: A key to adaptation in a changing climate

In the context of climate change, landraces present immense potential for the genetic enhancement of maize to ensure food security (Frona et al. 2019). The rising incidence of drought across various regions worldwide poses a considerable challenge to modern agriculture (Wiebe et al. 2019). While a slight temperature increase may benefit crop yields in temperate regions, it could have adverse effects on food security in tropical and subtropical areas (Lobell and Burke 2008). Due to their broad adaptability and superior tolerance to environmental stresses, landraces serve as valuable genetic resources for breeding programs, offering greater resilience compared to modern cultivars (Wild et al. 2024). Their extensive genetic diversity plays a crucial role in enhancing adaptability and expanding the maize gene pool, particularly in terms of resistance to biotic and abiotic stresses, as well as improving nutritional quality and culinary attributes (De Kort et al. 2021). Advances in genomic technologies have facilitated the exploration of allelic variation and molecular mechanisms governing adaptation and agronomic traits in maize landraces (Corrado and Rao 2017; Guan et al. 2022). Additionally, landraces are rich in secondary metabolites such as carotenoids and phenolics, which contribute to stress tolerance (Guzzon et al. 2021; Palacios-Rojas et al. 2020; Elisa et al. 2022). They also hold promise for improving quality traits in modern maize cultivars (Tamang et al. 2024).

Globally, landraces are being extensively utilized to enhance maize breeding programs (Prasanna 2010). Research by Reid et al. (1990) on maize races from Mexico revealed distinct adaptations to different altitudes and resistance to the European corn borer (*Ostrinia nubilalis*). Furthermore, the Mexican landraces Nal-tel, Chapalote and Palomero exhibit resistance to maize weevil (*Sitophilus zeamais*) (Arnason 1994). The Chinese maize cultivar Dan340, derived from the landrace Lvda Red Cob, possesses multiple beneficial traits, including disease and lodging resistance, high combining ability, and broad adaptability (Zhao et al. 2022).

Another significant landrace, 'Michoacan-21' from Mexico, has demonstrated remarkable recovery from severe drought stress due to the presence of the *latente* gene (Sharma 2005). This landrace exhibits resistance to permanent seedling wilting and tissue desiccation, with high transpiration under irrigation and reduced transpiration under stress conditions. Similarly, the Mexican landrace GalTrini and SITexas from Nuevo León have been identified as highly tolerant to water deficit (Gonzalez-Hernandez et al. 2021). In Africa, Nigerian landraces originating from Burkina Faso (TZm1162, TZm1167, and TZm1508) and Togo (TZm1472) have shown exceptional tolerance to drought and heat stress (Nelimor et al. 2020). Additionally, 'Tuxpeño Sequia' is a highly productive, early-maturing, drought-tolerant lowland maize race that thrives in fertile soils and is widely used in breeding programs.

Many maize landraces from rural Africa possess high nutritional value and contain genes that enhance tolerance to adverse conditions such as drought, salinity, and extreme temperatures (Dwivedi et al. 2016; Yang et al. 2019). The multiple aleurone layer (MAL) present in landraces like 'Coroico' (a South American race of floury maize), 'San Martin-105,' and 'San Martin-119' facilitates higher accumulation of essential minerals such as iron and zinc (Wolf et al. 1972; Lim and Yi 2019; Paulsmeyer and Juvik 2023). Another significant landrace, 'Burr's White,' was identified in the '100 Generations of Corn' experiment at the University of Illinois for its high protein, oil, and fatty acid content (Hopkins 1899; Dudley and Lambert 2004). The selected strains from this study were later utilized to identify quantitative trait loci (QTLs) associated with enhanced protein and fatty acid composition (Willmot et al. 2006). Moreover, research conducted by Daood et al. (2003) on the germplasm collection at the Institute for Agrobotany, Hungary, identified landraces with high carotenoid concentrations. A list of landraces with traits important for climate change adaptation is given in Table 1.

The development of doubled haploid (DH) lines derived from maize landraces has demonstrated significant potential, as some of these lines exhibit grain yields comparable to those of elite cultivars (Strigens et al. 2013). The successful introgression of landrace-specific DH lines into elite maize varieties suggests that eliminating potentially harmful alleles during DH line development may enhance genetic stability. Furthermore, the significant genetic distance between landrace-derived DH lines and elite germplasm underscores their potential to broaden the genetic base of modern maize (Strigens et al. 2013). These DH lines are also considered ideal resources for association mapping and allele mining due to their rapid reduction in linkage disequilibrium (LD) and minimal population structure.

The continued cultivation and preservation of maize landraces by farmers are largely driven by intrinsic, relational, and instrumental values (Monroy-Sais et al. 2024). However, research on effectively integrating these values into broader agricultural policies remains limited. The emphasis on maximizing yield and profit under the 'Green Revolution' model has negatively impacted agro-biodiversity and farmer livelihoods worldwide (Mulyoutami et al. 2023). Despite extensive efforts to collect and conserve maize landraces since the 1940s, many unnamed races have already disappeared (Curry 2022). This loss of genetic diversity has highlighted the urgent need for landrace conservation (Monroy-Sais et al. 2024).

One of the most extensive collections of maize landraces is maintained at the Wellhausen-Anderson Maize Genetic Resource Centre at CIMMYT in Mexico, which holds over 27,000 maize accessions from 64 countries, representing approximately 90% of the maize diversity in the Americas (Wen et al. 2011). In India, the National Bureau of Plant Genetic Resources (NBPGR) conserves nearly 9,000 maize accessions, primarily from the North Eastern Himalayan (NEH) region and Northern West Bengal. Of these, approximately 60% consist of landraces and populations.

Recognizing the significance of maize landraces, a segmented seed system that integrates both improved landraces and modern maize hybrids has been proposed (Hellin et al. 2014). Under this model, the public and private sectors would continue to provide improved maize varieties. At the same time, other stakeholders, including farmers, could produce and distribute seeds of improved landraces for sale and exchange. In countries such as Costa Rica and Honduras, farmers have shown a strong preference for hybridizing improved maize varieties with landraces (Almekinders et al. 1994). This hybridization process, known as 'creolization,' has resulted in the development of 'Criollo' varieties, which provide smallholder farmers with access to both modern genetic advancements and local adaptation benefits without requiring annual seed purchases (Bellon and Risopolous 2001).

Maize diversity in the Indian Himalayas

Grant and Wellhausen (1955) conducted studies on maize landrace diversity in India, revealing substantial variability

Table 1. List of important landraces from different countries which have been used in breeding programs as a source of tolerance to different biotic and abiotic stresses, nutritional quality and special traits

Name of the landrace(s)	Country of origin	Traits	Reference(s)
Nal-tel, Chapalote, and Palomero	Mexico	Resistance to maize weevil (*Sitophilus zeamais*)	Arnason 1994
Michoacan-21	Mexico	Drought tolerance due to presence of *latente* gene	Sharma 2005
GalTrini, SITexas, and Tuxpeño Sequia	Mexico	Drought tolerance	Gonzalez-Hernandez et al. 2021
San Martin-105 and San Martin-119	Peru	Presence of Multiple Aleurone Layer (MAL); higher accumulation of essential minerals such as iron and zinc	Lim and Yi 2019; Paulsmeyer and Juvik 2023
Coroico	South America	Presence of Multiple Aleurone Layer; higher accumulation of essential minerals such as iron and zinc	Wolf et al. 1972
Burr's White	United States of America	High protein, oil, and fatty acid content	Hopkins 1899; Dudley and Lambert 2004
TZm1162, TZm1167, TZm1472, and TZm1508	Nigeria	Tolerance to drought and heat stress	Nelimor et al. 2020
Lvda Red Cob	China	Disease and lodging resistance, high combining ability, and broad adaptability	Zhao et al. 2022
Poorvi Betapa, Arun Tepi, Murli, Tirap Nag-Sahypung, and Alok Sapa	India	Popcorn	Kumar et al. 2015
Mimban	India	Waxyness (high amylopectin)	Rathod et al. 2019
Sikkim Primitive (Murali Makai)	India	High prolificacy	Prakash et al., 2021
Gurez local	India	Cold tolerance	Ramazan et al. 2023

in the North Eastern Himalayan (NEH) region and the North-Western Highlands. The NEH region serves as a rich reservoir of maize landrace diversity, offering adaptability to a wide range of agro-climatic conditions. At Punjab Agricultural University (PAU), Ludhiana, a composite variety named 'Parbhat' was developed using Suwan-1, a well-known open-pollinated variety (OPV) from Thailand. This variety exhibits high yield potential, stable performance, and resistance to multiple diseases (Dhillon and Prasanna 2001; Dhillon et al. 2002).

Similarly, ICAR-Vivekananda Parvatiya Krishi Anusandhan Sansthan (VPKAS), Almora, has developed hybrids' Him-128' and 'Him-129' by utilizing various landraces from Jammu & Kashmir and Uttarakhand (Prasanna et al. 2010). Additionally, Govind Ballabh Pant University of Agriculture & Technology (GBPUAT), Pantnagar, has developed an OPV named 'Pant Composite Makka-4' using popular maize landraces (DLR-1, DLR-2, and DLR-3) collected from Uttarakhand.

Maize landrace diversity in North-Eastern Himalayas

The remarkable diversity of maize in the Indian Himalayan region has led to speculation that maize may have originated in Asia (Anderson 1941). While it is widely believed that maize was introduced to the Old World following Columbus's discovery of America (Mir et al. 2013), the genetic and morphological diversity of Himalayan landraces, particularly those adapted to the North Eastern Himalayan (NEH) region, challenges this notion. Some researchers suggest a pre-Columbian introduction, supported by mentions of maize grains in Vedic literature (Randhawa 1980; Singh et al. 2022). Additionally, a few ancient Indian and Chinese texts dating back to the 5th and 13th centuries AD, respectively, indicate an early presence of maize prior to Portuguese influence. The carvings of maize-like structures on Hoysala temple sculptures in Karnataka are also cited as potential evidence, though this remains debated.

Despite the limited historical literature on maize cultivation in the Indian subcontinent, studies on the distinct heterochromatic knobs of NEH landraces differentiate them from New World maize genotypes. Instead, these landraces resemble Mexican teosinte and primitive maize germplasm from the Caribbean and Andean highlands, suggesting a pre-Columbian introduction followed by its spread across Southeast Asia (Kumar and Sachan 1993; Prasanna and Sharma 2005).

The maize landrace *Sikkim Primitive* was first collected by N.L. Dhawan in the 1960s, who designated it as *Sikkim Primitive* (Dhawan 1964). This primitive maize group, primarily consisting of various popcorn races, is widely distributed across the Eastern Himalayan region (Kumar et al. 2015). Examples include Poorvi Betapa, Arun Tepi, Murli, Tirap Nag-Sahypung, and Alok Sapa (Kumar et al. 2015). The prevalence of popcorn types, high prolificacy, and drooping tassel traits in most NEH landraces indicates primitive characteristics, distinct from the widely introduced New World flint-maize genotypes.

The presence of waxy maize traits in Southeast Asia, including the NEH region, is atypical of New World flint and dent maize but resembles Aegean (Greek) maize varieties. This suggests an ancient trans-Atlantic introduction from the Americas to the Mediterranean, followed by a spread through the Silk Route to Southwest China, and subsequently into Southeast Asia due to favorable ecological conditions (Anderson and Brown 1952; Sorenson and Johannessen 2004). Furthermore, the discovery of maize cobs in ancient tombs in China's Sichuan province, along with the rich maize diversity in the Himalayan highlands—including China, India, Nepal, Bhutan, and Myanmar—supports the hypothesis of a trans-Pacific introduction, making Asia a potential convergence point for both trans-Atlantic and trans-Pacific maize dispersal (Anderson and Brown 1952).

Several NEH landraces have been extensively collected and studied by researchers both before and after India's independence (Anderson 1945; Stonor and Anderson 1949; Ono and Suzuki 1956; Dhawan 1964; Thapa 1966; Singh 1977; Sachan and Sarkar 1982; Sharma et al. 2010; Rahman and Karuppaiyan 2011; Kumari et al. 2017; Sharma and Pradhan 2023). NEH maize landraces have been characterized at the morphological and molecular levels (Prasanna 2010). Using isozyme markers, Bhat and Chandel (1998) revealed similarities between Indian maize landraces cultivated in the NEH region and Mexican landraces. Baruah et al. (2024) documented extensive genetic diversity among 83 NEH-based maize landraces for various morphological traits and biochemical parameters, including anthocyanins and phlobaphenes.

Additionally, phenotypic and molecular analyses were conducted on 132 maize landraces, including 69 accessions from eight NEH states (Prasanna and Sharma 2005). Prasanna et al. (2005) provided the first comprehensive molecular characterization of 27 Indian maize landraces from various agro-ecological zones, 10 of which were from the NEH region. Sharma et al. (2010) later characterized 48 landraces, including Sikkim Primitive, for prolificacy using SSR markers and a population bulk DNA fingerprinting approach. Further SSR-based diversity studies were carried out on 48 selected NEH landraces (Singode and Prasanna 2010). Natesan et al. (2020) characterized 26 maize landraces from the NEH region for the *crtRB1* gene using a gene-based marker and identified 10 landraces possessing the favorable *crtRB1* allele, marking them as rich sources of provitamin A.

Sikkim Primitives: A unique maize landrace of NEH

Of the various landraces from North Eastern Himalayan region, landraces from Sikkim province have raised special interest among maize breeders. The most important maize landraces of Sikkim include *'Murali Makkai', 'Seti Makkai', 'Pahenlo Makkai', 'Rato Makkai', 'Baiguney Makkai', 'Lachung Makkai', 'Sherung', 'Tempo Rinzing', 'Garberey', 'Khukurey', 'Kalo Makkai', 'Putali Makkai', 'Chaptey Makkai', 'Kuchungtakmar Makkai', 'Bancharey Makkai', 'Kuchungdari'* and *'Gadbade Makkai'* (Prasanna 2010). Among these, *Sikkim Primitive,* also known as Murali Makkai, is distinct, exclusively used for commercial offerings by the Buddhist community in the area (Dhawan 1964). Two accessions, *viz*., *Sikkim Primitive*-1 (purple grains) and *Sikkim Primitive*-2 (yellow grains), were first collected in the 1960s from Sikkim (Dhawan 1964). It grows at mid-elevations of 2000 to 2700 m in the humid tropical cloud forest of Sikkim and is believed to be a primitive form of ancestral maize. The key features of the *Sikkim Primitive* include 7-9 ears per plant compared to 1-2 ears per plant in modern maize (Sachan and Sarkar 1982). It also lacks apical dominance and possesses uniformity in ear size, popcorn-type kernels, and tall plants with drooping tassels for effective fertilization (Figure 1). *Sikkim Primitive* also possesses relatively thin but strong culms, synchronous growth and maturity of all ears, and photo-sensitivity (Anderson 1945; Singh 1977). The ears of the *Sikkim Primitive* are small, thin and cylindrical, occasionally tapering, measuring between 6 to 12 cm in length, featuring 8 to 12 irregular rows with small popcorn-type kernels (Singode and Prasanna 2010). A detailed account of the morphological difference between *Sikkim Primitive* landrace, modern maize inbreds and teosinte is given in Table 2.

Genetic dissection of prolificacy in Sikkim Primitive

The Sikkim Primitive landrace has been extensively analyzed at the morphological, cytological, and molecular levels. Notably, its morphological characteristics suggest a closer relationship with maize (Sachan and Sarkar 1982). This landrace was categorized as 'primitive' due to its high prolificacy, sensitivity to photoperiod, small popcorn-type grains, and significant pollen production. Kapoor et al. (2022) recently conducted morphological trait characterization of Sikkim Primitive, while Pandey et al. (1986) investigated variations in heterochromatin among its chromosomes. Additionally, Kumar and Sachan (1996) evaluated genetic diversity in pachytene knobs among 41 maize landraces from the NEH region, including Sikkim Primitive. Although discovered in the 1960s, the genetic basis of prolificacy in Sikkim Primitive remained unclear for decades, largely due to its heterogeneous nature, a common characteristic of cross-pollinated crops like maize.

The prolificacy in Sikkim Primitive results from multiple developmental modifications in maize, including axillary

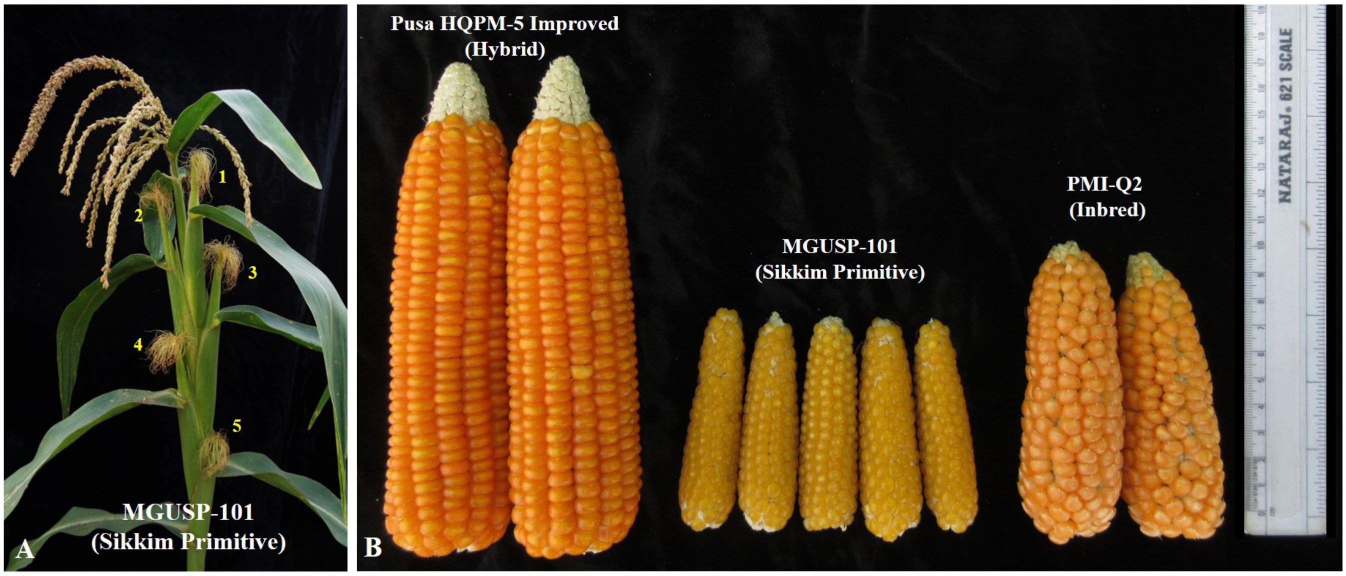

Fig. 1. A. Plant architecture of Sikkim Primitive (MGUSP-101) grown at Delhi, B. Ear and grain characteristics of Sikkim Primitive (MGUSP-101) and its comparison with ears of inbred and hybrid

Table 2. Major morphological differences between Maize, Teosinte, and Sikkim Primitive landrace

S. No.	Trait	Maize	Teosinte	Sikkim Primitive
1.	Tillering habit	Absent	Present, bushy habit	Absent
2.	Primary branch	Shortened, internodal length is highly reduced, leaves developed into cob sheath, Tipped by female inflorescence (ear).	As main culm, tipped by male inflorescence (tassel)	Shortened, internodal length is highly reduced, leaves developed into cob sheath and covering the female inflorescence (ear). Sometime tip of inflorescence is male (tassel) and it leads to self-fertilization.
3.	Secondary branch	Not present	Developed as female inflorescence (ear)	Not present
4.	Number of ears per plant	1-2	20-100	7-9
5.	Number of seeds per ear	100-400	8-10	100-200
6.	Presence of cupulate (stony) fruit case over seeds	Not present (naked kernel)	Present	Not present (naked kernel)
7.	Paired spikelet	Present	Absent	Present
8.	No. of rows of kernel	4-7 paired rows (10-14 rows) (polystichous)	1 pair rows (2 rows) (distichous)	4-7 paired rows (10-14 rows) (polystichous)
9.	100-Kernel Weight	20-30 g	6-8 g	9-10 g

bud initiation and maintenance, transformation of these buds into primary branches, and the subsequent conversion of primary branches into female inflorescences (Prakash et al. 2019). Several physiological, metabolic, and environmental interactions regulate this process, with crucial factors such as nutrient availability, hormonal equilibrium at nodes, auxin-cytokinin ratios, strigolactone signaling, physiological stress responses (drought, heat, salinity), cell cycle regulation, light exposure, source-sink balance, and crop density playing significant roles (McSteen et al. 2000; Eveland et al. 2010; Kebrom and Brutnell 2007; Prasanna 2010). Given the importance of understanding these factors, research at ICAR-Indian Agricultural Research Institute (IARI), New Delhi, led to the development of an inbred line (MGUSP-101) through repeated selfing of Sikkim Primitive (IC-565866). MGUSP-101 retains the original landrace's high prolificacy and popcorn kernel traits.

In teosinte, a species known for its prolificacy and ability to produce over 50 small ears per plant, the *tb1* gene has been linked to branching regulation (Studer et al. 2011). *Tb1* encodes a *TCP* (*Teosinte branched1* of maize; *Cycloidea* of snapdragon; *Proliferating cell nuclear antigen factor1 and 2* of rice) domain transcription factor involved in meristem growth, floral primordia initiation, and cell cycle regulation (Cubas et al. 1999; Lukens and Doebley 2001). Functioning as the master regulator of plant and inflorescence architecture, *tb1* codes for a bHLH DNA-binding protein with three conserved domains (Lukens and Doebley 2001). It suppresses axillary bud growth along the main stem, influencing female inflorescence formation in maize (Doebley 2004). Unlike teosinte, maize exhibits higher *tb1* expression, leading to reduced branching due to the presence of an approximately 12 kb enhancer region (~58-69 kb upstream of the *tb1* coding sequence) (Doebley et al. 1997; Clark et al. 2006). Maize-specific insertions of Hopscotch (~58-64 kb) and Tourist (~64-69 kb) retrotransposons within this enhancer region distinguish it from teosinte (Zhou et al. 2011; Studer and Doebley 2012; Vann et al. 2015).

To determine whether *tb1* variation contributes to Sikkim Primitive's prolificacy, sequencing of the *tb1* gene in MGUSP-101, five maize inbreds (LM17, HKI1128, BML7, UMI1200, and CML425), and four teosinte accessions (*parviglumis*, *perennis*, *luxurians*, and *mexicana*) was performed (Prakash et al. 2020). Results showed that the Hopscotch and Tourist transposable elements were present in maize inbreds, including MGUSP-101, but absent in wild relatives. This indicated that an alternative regulatory mechanism beyond *tb1* might govern prolificacy in Sikkim Primitive (Prakash et al. 2020).

Further investigation through genetic analysis of crosses between MGUSP-101 and four non-prolific inbreds (LM13, BML7, HKI161, and HKI1128) revealed a quantitative inheritance pattern with duplicate epistasis-type non-allelic interactions. Dominance × dominance effects were more pronounced than additive × additive and additive × dominance effects. Major gene block analysis suggested the presence of at least one significant gene/QTL influencing prolificacy (Prakash et al. 2019). Additional $F_{2:3}$ mapping populations were developed by crossing MGUSP-101 with two non-prolific inbreds, HKI1128 and UMI1200, leading to the identification of a major QTL (bin: 8.05) explaining 31.7% and 29.2% of phenotypic variation, respectively. This novel QTL was designated as '*qProl-SP-8.05*' (Prakash et al. 2021). Unlike the previously reported QTL, *prol1.1*, located on chromosome 1, which contributed to multiple ears from a single node (Wills et al. 2013), the *qProl-SP-8.05* QTL was associated with ear development at each node in Sikkim Primitive.

To further elucidate the genetic framework of Sikkim Primitive, whole-genome sequencing was conducted on MGUSP-101 along with three non-prolific (HKI1128, UMI1200, and HKI1105) and three prolific (CM150Q, CM151Q, and HKI323) inbreds (Prakash et al. 2024). This analysis identified 942,417 SNPs, 24,160 insertions, and 27,600 deletions. Functional classification of gene-specific mutations in Sikkim Primitive revealed 10,847 missense (54.36%), 402 nonsense (2.015%), and 8,705 silent (43.625%) mutations. The landrace exhibited 666,021 transitions and 279,950 transversions, with (G to A) being the most frequent (215,772) and (C to G) the rarest (22,520). Notably, unique alleles were identified in the gene encoding *polygalacturonate-4-a-galacturonosyltransferase*, an enzyme linked to pectin biosynthesis, cell wall organization, and sugar metabolism. Additionally, *Zm00001eb365210*, encoding glycosyltransferases, emerged as the potential candidate gene underlying '*qProl-SP-8.05*' for prolificacy in Sikkim Primitive. High-impact nucleotide variations were detected in *ramosa3* (*Zm00001eb327910*) and *zeaxanthin epoxidase1* (*Zm00001eb081460*), genes implicated in branching and inflorescence development (Prakash et al. 2024). These candidate genes are currently being validated and introgressed into elite maize lines at IARI, New Delhi, to enhance prolificacy traits.

Way forward

Despite the presence of ample genetic diversity in maize landraces found in NEH regions, their utilization in maize breeding is still a major bottleneck. A strong pre-breeding activity needs to be initiated for derivation of homozygous genetic stocks with the unique trait(s) specific to each of the landraces. DH technology should be intensively utilized to derive homozygous inbreds from each of the unique landraces. Inheritance study followed by identification of locus (loci) underlying a particular trait needs to be undertaken systematically. Validation of gene(s) followed by its introgression through molecular breeding would accelerate the genetic improvement in maize.

Authors' contribution

All the authors have contributed equally.

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