POTATO TUBER DRY MATTER: A CRITICAL TRAIT FOR BREEDING, PROCESSING AND PRODUCTIVITY

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ABSTRACT: Potato (*Solanum tuberosum* L.) is a globally important staple crop valued for its versatility and high carbohydrate content. Tuber dry matter content (TDM) typically comprising 20% of freshly harvested tubers, is a critical trait influencing processing quality, nutritional value and marketability. TDM is closely associated with specific gravity and varies significantly across cultivars and is shaped by genetic and environmental factors, including agronomic practices and storage conditions. High TDM is essential for processing industries particularly chips, French fries and dehydrated products due to higher product yield, lower oil uptake and better texture. While 18–20% TDM is adequate for canning, levels exceeding 20% are optimal for most fried and dried products. Despite its importance, breeding for high TDM presents challenges due to its quantitative inheritance and strong genotype- by-environment interactions. Moreover, increased TDM may compromise other traits, such as tuber yield and culinary quality, including disintegration during boiling. These trade-offs complicate breeding decisions and demand a balanced approach that integrates genetic, physiological and agronomic strategies. This review critically examines the significance of TDM in potato breeding and processing, explores its genetic and environmental determinants and highlights current challenges and future opportunities in developing high-TDM cultivars. By enhancing our understanding of this complex trait, we can better align breeding goals with industry needs and consumer preferences, ultimately improving potato productivity and value across the supply chain.

KEYWORDS: Potato, Tuber Dry Matter, Specific Gravity, Processing Quality, Breeding

INTRODUCTION

Potatoes are among the most highly consumed food crops worldwide, with high per capita consumption across many regions. As the fourth most important food crop after rice, maize and wheat, the potato holds the distinction of being the world's most important vegetable. Its high nutritional value, favorable harvest index and good yield potential make it an ideal crop for addressing global challenges related to population growth, food security and nutritional needs.

Following its global dissemination during the colonial era, the potato gained widespread acceptance as a calorie-dense food. Historians have highlighted its critical role in influencing demographic patterns, famine events and mass migration.

The "potato influence" of the medieval period played a transformative role in shaping global population dynamics and political

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history. Over time, significant efforts have been made to improve the crop's adaptability to diverse agroecological zones, enhance its yield potential and expand its end-use applications. Although potato yields increased by about 50% between 1966 and 2016, this gain is relatively modest compared to those achieved in maize, rice and wheat over the same period. However, when yields are compared on a dry weight basis, potato production increase (3.92 t/ha) is quite comparable to that of maize (4.79 t/ha), wheat (2.90 t/ha) and rice (3.94 t/ha) (Bradshaw 2021). Yield improvements have been driven by advances in crop improvement, the use of modern fertilizers, disease-free seed, plant protection chemicals and agricultural mechanization.

Potato tubers consist of 75–85% water and 15–25% tuber dry matter (TDM). Despite their high moisture content, potatoes yield more edible energy, protein and dry matter per unit area and time than cereal crops (Wassu, 2017). However, tuber dry matter content has received comparatively less attention in potato breeding programs, as high TDM is often viewed primarily as a requirement for specific processing purposes such as chip and fry production. In general cultivation, varieties with higher overall yield are typically preferred by growers, unless specific traits such as disease resistance, stress tolerance, or industrial applications like starch extraction are prioritized. In India, for instance, potato varieties with TDM of 18–20% are considered suitable for table purposes (boiling/baking), while those with TDM above 20% are recommended for processing into chips, French fries and flakes (Souza and Silva 2003).

It also reflects the cumulative nutritive content of the tuber, including starches, carbohydrates, fats, proteins, minerals and vitamins. Its high correlation with starch content, offer higher caloric density. While the average potato provides approximately 70 kcal per 100 g fresh weight (Trawczyński 2016), tubers with higher TDM provide substantially greater calorific value. This has important implications across multiple dimensions, enhanced nutritional productivity per unit land area, improved input-use efficiency (irrigation, harvesting and transport) and economic benefits throughout the value chain.

Besides, TDM also significantly affects texture, taste, resistance to mechanical damage and the overall processability of tubers (Thygesen *et al.,* 2001; Tarn *et al.,* 2010) which influence consumer preferences, culinary suitability and market acceptance.

Given these considerations, it becomes imperative to focus on this important characteristic of potatoes at various levels ranging from breeders and agronomists to growers and consumers. This review aims to comprehensively examine the importance of TDM in potatoes, a trait of critical relevance across breeding, cultivation, storage, processing and consumption. It synthesizes current knowledge on the physiological, genetic, agronomic and environmental factors influencing TDM, discusses methods of its estimation and highlights recent advances in molecular and genomic tools for improving this trait. Furthermore, the review explores TDM's role in determining processing quality, nutritional value and economic efficiency. By consolidating these diverse aspects, the review advocates for the strategic integration of TDM into breeding and crop management programs to meet evolving industry and consumer demands.

POTATO TUBER AS A STORAGE ORGAN

Potato tubers, the edible part of the plant, are metabolically active, specialized stem structures that serve not only as storage organs but also support vegetative propagation. These storage organs significantly influence the tuber's physical characteristics and chemical composition. Being rich in metabolically active plastids, tubers synthesize a variety of compounds through plastidic pathways ranging from primary metabolites to complex secondary metabolites. These compounds contribute not only to the organoleptic properties of the tubers but also provide physiological advantages in terms of tuberization and environmental adaptation (Katan and De Roos 2004; Navarre *et al.,* 2009). TDM, specific gravity and starch content in potato increase progressively from planting to maturity. This rise stabilizes upon physiological maturity, which is marked by the senescence of aerial plant parts leading to a decline in photosynthetic activity and, consequently, TDM accumulation (Kumlay *et al.,* 2002). Physiological maturity is marked by a peak in TDM indicating full tuber development (Sabba and Lulai, 2002; Bussan *et al.,* 2009). Mature tubers are also characterized by lower levels of reducing sugars which is beneficial for both storage and processing quality (Driskill *et al.,* 2007). Furthermore, tubers with higher concentrations of dry matter, starch and calcium exhibit increased resistance to mechanical stress, a trait linked to specific structural attributes of their cells. Calcium in particular has been shown to enhance cell wall integrity by strengthening the bonds between cell wall polymers, thereby stabilizing the overall structure (Koch *et al.,* 2019).

ESTIMATION OF DRY MATTER

Estimating TDM is a fundamental step in all potato breeding and evaluation programs due to its close association with processing quality and nutritional content. A common method involves selecting five randomly drawn tubers from each variety. These tubers are sliced horizontally and half of each tuber is finely chopped and homogenized. A 50 g sample from each variety, in triplicate, is then dried in a hot air oven at 80°C for 72 hours until a constant weight is reached, indicating complete moisture removal (Luthra, 2003). Although direct TDM estimation can be time-consuming, it is highly correlated with specific gravity, enabling indirect assessment using a 3–5 kg tuber sample (Tawfik *et al.,* 2002; Kumar *et al.,* 2005). This method, widely used for large-scale evaluations, typically employs the specific gravity measurement technique outlined by Storey and Davies (1992), in which tuber weight is measured in air (x) and underwater (y) to calculate specific gravity using the formula SG = x/(x–y). A specific gravity value of 1.095 generally corresponds to a TDM of approximately 24%. The measurements can be expressed as a percentage of total fresh weight or as a ratio of dry to fresh mass, as described by Mostofa *et al.,* (2019). Commercial specific gravity balances with capacities up to 10 kg are also used for this purpose.

In recent years, advancements in analytical tools have enabled the development of more precise and industry-friendly methods for TDM estimation. Processing industries now widely employ equipment specifically designed to assess specific gravity. Additionally, near-infrared (NIR) spectroscopy has gained popularity for its rapid and non-destructive estimation capabilities. In this method, NIR spectra in the 700–1100 nm range are acquired and analyzed using partial least squares (PLS) regression to build predictive models for specific gravity estimation (Scanlon *et al.,* 1999). VIS–NIR spectroscopy coupled with a 1D-convolutional neural network

(1D-CNN) for online prediction of potato dry matter content has been evaluated by Guo et al. (2024) for TDM estimation. The model automatically extracted spectral features without manual preprocessing and demonstrated high prediction accuracy, robustness, and rapid processing, making it suitable for industrial applications. While non-destructive assessment techniques offer several advantages, they also present important limitations. These include the need for handling and analyzing large and complex datasets, frequent calibration for changes in setup, high costs associated with purchase, maintenance and repair. Additionally, their performance can be affected by physical and environmental factors such as lighting conditions, cultivar, seasonal variation, optical alignment, sample size and temperature (Wang *et al.*, 2023).

Non-destructive techniques, such as imaging and spectroscopy, are less accurate than the direct dry matter assessment carried out in lab, enable rapid, high-throughput comparative quality inspection of large seed lots received from the field and storage and are suitable for high end processing industries. Breeding pipelines may rely on simpler dry matter estimation methods in the early generations and direct dry matter based or specific gravity based estimations to ensure development of the desirable potato varieties.

TUBER DRY MATTER CONTENT GOVERNS POTATO USE

The quality of potatoes is a critical factor in determining market acceptance. Consumer perception is primarily influenced by external attributes such as appearance, colour, size, shape, and the presence or absence of defects. In addition, texture, flavour, and nutritional value are critical internal quality parameters that significantly influence consumer preference and overall marketability. TDM is closely associated with internal quality attributes like texture and the end-use suitability of potato varieties (Table 1). A mealy texture corresponds to high TDM levels, whereas a waxy texture is associated with lower TDM.

TDM is the most important criterion for processing potatoes, significantly influencing both product recovery and quality. High TDM varieties yield better outputs for dehydrated products such as flakes, starch and cubes compared to those with low TDM which are suitable for boiling and salads. Additionally, it affects multiple processing traits, including crispiness, color, oil absorption, flavor and final product texture (Marwaha *et al.*, 2008). Low-TDM tubers absorb more oil during frying, leading to greasy and sticky-textured products. Since oil constitutes a major cost in fried product manufacturing, selecting varieties with optimal TDM can substantially reduce processing expenses. Desirable traits

Table 1. Relationship between tuber dry matter and optimum use (Mosley and Chase 1993)

Specific gravity	Dry matter %	Texture	Typical uses
Below 1.060 (very low)	Below 16.2	Very soggy	Pan frying, salads, canning
1.060-1.069 (low)	16.2-18.1	Soggy	Pan frying, salads, boiling, canning
1.070-1.079 (medium)	18.2-20.2	Waxy	Boiling, mashing, fair to good for chip processing and canning
1.080-1.089 (high)	20.3-22.3	Mealy, dry	Baking, chips, frozen French fry, some cultivars tend to slough when boiled
Above 1.089 (very high)	Above 22.3	Very mealy or dry	Baking, frozen French fry, chip, tendency to produce brittle chips and to slough when boiled

for processing-grade potatoes include high specific gravity, elevated TDM, low reducing sugars and high starch content (Kumar *et al.*, 2009; Wassu 2017).

In recent years, there has been a marked increase in breeding efforts aimed at developing processing-specific cultivars. In India, a series of cultivars such as Kufri Chipsona-1, Kufri Chipsona-2, Kufri Chipsona-3, Kufri Chipsona-4, Kufri Chipsona-5, Kufri Himsona, Kufri Frysona, Kufri FryOM and Kufri Sangam have been developed to meet the specific needs of the processing industry.

Nutritional quality is further influenced by the composition of starch fractions, namely rapidly digestible starch (RDS), slowly digestible starch (SDS) and resistant starch (RS). These fractions influence the glycemic response and digestion rate (Englyst et *al.*, 1992), underscoring the importance of not only evaluating the quantity but also the quality of TDM to breed nutritionally enriched varieties with specific health benefits.

TUBER DRY MATTER DISTRIBUTION WITHIN A TUBER

Tuber dry matter (TDM) content varies not only between tubers on the same plant but also within different regions of an individual tuber. The highest concentration of TDM is found in the outer cortex, apical and stem end regions, while the central pith typically contains the lowest levels (Pritchard and Scanlon 1997). According to Iritani and Weller (1973) moisture stress during the growing season contributes significantly to this non-uniform distribution. Moreover, TDM and sugar distribution within tubers can shift during storage. While the flesh of the tuber is rich in TDM and total soluble solids, the peels are more concentrated in protein, fiber, ash and minerals with the exception of magnesium. Varieties with uniform starch distribution are preferred for the development of processing cultivars, as they ensure uniform colour and quality in the final processed products.

FACTORS AFFECTING TUBER DRY MATTER

Genotypic Variation: TDM exhibits a strong genotypic influence, although it remains susceptible to environmental conditions (Tsegaw, 2011). Variation in intra-tuber TDM distribution is also genotype-dependent (Grewal and Uppal 1989; Pritchard and Scanlon 1997; Marwaha *et al.*, 2010; Wayumba *et al.*, 2019; Kajunju *et al.*, 2022; Islam *et al.*, 2022). As a highly heritable trait, TDM demonstrates stability over multi-year evaluations with values ranging from <16% to >22% depending on the variety. It is essential to select appropriate cultivars for specific uses such as processing. Diploid pre-breeding populations have been reported to show wider variation in total dry matter and glucose content due to their higher genetic diversity and limited selection as compared to advanced tetraploid lines which are more uniform as they have already undergone multiple cycles of selection for desirable quality traits (Bonierbale *et al*., 2003). Early-maturing genotypes generally have lower TDM due to a shorter photosynthate accumulation period, while very late types may sometimes display poor TDM allocation between foliage and tubers (Haverkort and Kooman 1997). The released potato processing varieties having higher TDM are mostly of late maturing type.

Gupta et *al.*, (2015) reported TDM in 44 Indian potato varieties, ranging from 16% in Kufri Khyati and Kufri Pukhraj to 24% in Kufri Kundan, Kufri Himsona and Kufri

Frysona. Floury texture and flavor showed positive correlations with TDM (r = 0.33*, r = 0.32*). Similar ranges have also been reported by Luthra et *al.,* (2018).

Environmental Variation: TDM is influenced by genotype-environment interactions. Mthembu et *al.*, (2022) noted the combined impact of genotype, water availability and growth stage on TDM, yield and tuber size. Spring-grown tubers usually show higher TDM and starch but lower reducing sugars and polyphenols than autumn-grown ones (Freitas et *al.*, 2012). In Peru, potatoes grown at 3273 masl exhibited higher TDM and better TDM partitioning than those at 230 masl (Victorio et *al.,* 1986).

Mazurczyk *et al.*, (2009) found that cooler, more humid conditions with low radiation supported better TDM accumulation. TDM content in the same variety fluctuated across years, seasons and locations due to planting time, temperature and soil moisture. In India, longer durations are needed for achieving suitable TDM and low reducing sugars in potatoes grown in the north-western and west-central plains (Gupta *et al.,* 2024). Salej *et al.* (2022) in the varietal evaluation of varieties released over time (Era trials) for quantifying realized genetic progress in Indian potato varieties reported that mean dry matter was high in the Eastern plains and West-Central plains whereas, the highest dry matter was observed in the hilly regions. Whereas the Eastern plains and West-Central plains of India depict cool night temperatures (8–14 °C), bright sunshine, low humidity, and controlled irrigation during tuber bulking which are important climatic factors promoting high total dry matter accumulation in potato. The high dry matter reported in hilly regions is merely on account of the long growing periods.

Temperature: Air temperature significantly affects both total and tuber-specific TDM. Studies on Bintje and Désirée show that rising air temperature reduces tuber TDM with distinct responses from stolons and secondary growth (Struik *et al.,* 1989). High day/night temperatures (31°C/29°C) reduce TDM and harvest index compared to lower regimes (19°C/17°C) (Lafta and Lorenzen 1995). Transient heat stress (>7 days) has been reported to increase TDM and reducing sugars, causing defects such as stem-end chipping (Busse *et al.,* 2019). While, Indian regions with mild night temperatures (>10°C) tend to produce high TDM and low reducing sugar content (Pandey *et al.*, 2009; Gupta *et al.*, 2024).

Radiation: Solar radiation better expressed as RUE (radiation use efficiency) plays a critical role in TDM accumulation by enhancing photosynthetic activity, translocation of photosynthates to the developing tubers thereby promoting early tuber initiation and efficient tuber bulking (Goudriaan and Monteith, 1990; Burstall and Harris, 1983; Ewing and Struik, 2010). TDM has been defined as the product of intercepted radiation (IR, MJ m^{-2}), radiation use efficiency (RUE, g MJ^{-1}) and the harvest index (HI, g g^{-1}) (Sandana *et al.*, 2023). TDM is both dependent of area of cultivation as well as the genotype (plant canopy and leaf architecture). Persistent cloud cover and frost reduce photosynthesis, moisture levels and TDM (Darabi and Mohammadi 2015). Elevated ozone has been reported to reduce starch content (Vandermeiren *et al.,* 2005), while increased CO_2 enhances TDM accumulation (Wheeler *et al.,* 1991).

Soil Type: Soil characteristics such as water-holding capacity, structure and fertility influence TDM directly or in combination with other factors. Drier soils may enhance TDM concentration but limit yield. Loamy soils with optimal moisture and temperature conditions support both yield and TDM. Clay loams support better TDM accumulation in wet conditions as compared to sandy soils on account of higher nutrient retention promoting growth. Loamy soils have been reported to offer highest productivities in potato and therefore the TDM on account of their optimum moisture and temperature relationships. While pH has no direct effect on TDM, it may affect yield and TDM per hectare. Generally, a pH range of 5.5 to 6.2 is considered optimal for potato growth and tuber development, as it promotes the uptake of essential nutrients. Deviations from this ranges create imbalances in nutrient uptake leading to reduction in tuber yield, quality and reduced dry matter.

Planting Date and Maturity: Early planting enhances TDM by maximizing photosynthetic activity during tuber initiation. Nevertheless, actual emergence date may be a more reliable indicator. In Meghalaya, mid-November planting resulted in the highest TDM in winter potatoes (Gogoi and Ray 2019). Mature tubers generally contain less reducing sugar and TDM but offer improved storage and lower susceptibility to damage (Driskill *et al.,* 2007).

Fertilizers: Increased soil fertility tends to reduce TDM (Vos 1997; Mazurczyk and Lis 2000; Bélanger *et al.,* 2001). Nitrogen application often boosts vegetative growth at the expense of TDM, particularly when extending maturity periods. El-Hadidi et al. (2017) reported that excessive nitrogen application delays tuber initiation, diminishes specific gravity, and decreases yields in certain cultivars. Splitting nitrogen does not significantly affect TDM (Sun *et al.,* 2012). Studies report no significant nitrogen effect on TDM (Sun *et al.,* 2012), while others show positive responses to calcium addition (Banerjee *et al.,* 2014) or variety-fertigation interactions (Bandana *et al.*, 2018). Potassium influences starch synthesis via activation of starch synthase. Xie and Wang (2022) reported available potassium showed the strongest positive correlation, followed by soil nitrate content, electrical conductivity, water content and available phosphorus. Similar observations also reported by Panique *et al.* (1997) and Koch *et al.* (2020). Arsenic contamination has been reported to lower TDM and starch levels (Haque *et al.,* 2018). Among the different forms of supplied Potash, Polyhalite followed by Sulphate of Potash reportedly increases TDM, while Muriate of Potash reduces it (Panique *et al.*, 1997; Roy *et al.,* 2017). Increased P availability in soils has also been correlated with high TDM, besides lowering total sugar content and higher contents of both starch and proteins (Leonel *et al.*, 2017). Nutrient uptake at 40 days after planting shows a strong positive correlation with total dry matter content, as it determines the plant's capacity for assimilate production and efficient partitioning to tubers (Da Carlos et al., 2020). The second half dose of nitrogen is generally recommended for application at this critical stage in potato to enhance tuber bulking. Organic fertigation supplemented with N and P reportedly has no effect on TDM (Prakash *et al.*, 2024; Alexopoulos *et al.,* 2019).

Chemical Applications: Biostimulants such as Green OK-Universal Pro and Asahi SL, alone or with herbicides like Avatar 293 ZC, enhance TDM and starch accumulation (Baranowska 2018). Gypsum and boron foliar spray applications have been reported to significantly improve TDM at optimized doses (Shirur *et al.,* 2021).

Irrigation Regime: Irrigation method and regime reportedly plays a profound effect on potato TDM, as it is a shallow root plant whose roots are mainly distributed in the soil surface and extremely sensitive to water stress. Reduced irrigation post-tuberization enhances starch and TDM but can lower yield (Carli *et al.*, 2014; Banerjee *et al.*, 2016). Drip irrigation is superior to furrow systems in increasing TDM and chip recovery (Sinha *et al.,* 2021). Irrigating up to 50% of tuber development has been reported to boost TDM and nutritional traits (Ierna and Mauromicale, 2022). In recent reports by Li *et al*. (2023) water deficit reduced flowering, tuber yield, dry matter and tuber size.

Biochemical Factors: Starch, constitutes upto 75% of TDM which enhances processing quality (Lister and Munro 2000; Bandana *et al.,* 2016; Burke 2012). Strong positive association of TDM have been reported with soluble protein (r = 0.76**) and ascorbic acid (r = 0.51*) (Luthra *et al.,* 2018). High TDM also negatively correlates with low reducing sugars and lower glycemic index (Kumar *et al.,* 2009). High TDM varieties like Agria, Aula, Herta, Aziza and Sante also feature favorable specific gravity and processing traits (Hassanpanah *et al.,* 2006). These are already being considered for improving potato quality and nutritional status of potato varieties.

Effect of Storage on Tuber Dry Matter (TDM)

Potatoes are a semi-perishable commodity that require proper storage to ensure a continuous supply during the offseason. Under controlled conditions of 2–4 °C and 95% relative humidity, tubers can be stored for over six months. Storage at low temperatures (2–4 °C) slows enzymatic and metabolic processes, thereby retarding starch degradation and minimizing TDM loss. However, extended low-temperature storage also increases sugar accumulation, which negatively affects processing quality. Long term low-temperature storage leads to sugar accumulation, a phenomenon known as cold-induced sweetening, which imparts an undesirable sweet taste in table potatoes and causes darkening and poor-quality chips during frying (Freitas *et al.,* 2012; Kaaber *et al.,* 2001). This is caused due the breakdown of starch stored in the amyloplasts through the phosphorolytic pathway involving phosphorylase and the hydrolytic pathway involving amylase into sugar phosphate compounds. These can be further converted into suberin for wound healing or into additional starch compounds during wound periderm formation (Geigenberger *et al.,* 2004). It is estimated that TDM losses over a seven-month period range from 1.6% to 4.3% under optimal storage conditions (Kaaber *et al.,* 2001).

Conversely, when tubers are stored at higher temperatures, they tend to lose moisture through respiration and evaporation, leading to a relative increase in TDM as a result of tuber shrinkage on account of reduced moisture content (Kaaber *et al.,* 2001). Further, as tubers break dormancy and begin to sprout, respiration rates further increase, enhancing the conversion of starch into reducing sugars, which are consumed during metabolic activity, contributing to a net reduction in TDM over time. Temperatures, around 8–12°C reportedly help maintain processing quality by reducing cold-induced sweetening and have been shown to slightly increase TDM content.

During storage, several physiological and biochemical changes affect tuber TDM content. As storage progresses, Improper storage conditions, such as poor ventilation, immature or damaged tubers, or excessively humid environments, can enhance respiration losses that exceed evaporative water loss, ultimately causing a decline in TDM (Heltoft *et al.*, 2016). Humidity levels during storage also play a critical role; maintaining optimal humidity around 95% helps reduce moisture loss and stabilize TDM content, whereas low or fluctuating humidity accelerates desiccation and respiration, resulting in variable effects on TDM.

GENETICS AND BREEDING FOR TDM

TDM in potato is a complex quantitative trait governed by multiple genes and significantly influenced by environmental conditions. Despite this complexity, TDM shows high heritability, making it a promising target for genetic improvement through both conventional and molecular breeding methods.

TDM is primarily controlled by general combining ability (GCA) rather than specific combining ability (SCA), indicating the predominance of additive gene effects. Bradshaw *et al.*, (2000) found that GCA variance for specific gravity (high correlation with TDM) was significantly higher than SCA variance. Additionally, narrow-sense heritability of TDM is high, enabling effective selection using full-sib family breeding strategies. TDM is also positively associated with essential processing traits such as fry color, making it a critical component in breeding programs targeting processing-quality potatoes (Islam *et al.*, 2022).

In breeding programs, high TDM is an important selection criterion alongside yield, disease resistance and agronomic performance. In breeding for processing varieties, parental lines are selected based on their dry matter potential and field performance. Screening for TDM is typically initiated in the early generations, such as F1C1, to identify elite clones, which are then multiplied in advanced generations to carry out replicated trials (Luthra *et al.*, 2020). The TDM is generally attributed a 10% score in the varietal score card for selecting a variety for release. The analysis by Salej et al. (2023) revealed very low and occasionally negative genetic gain for total dry matter content (TDM) in the Indian potato breeding programme over the last fifty years, indicating limited selection progress for this trait. This observation differs from Bradshaw (2021), who reported measurable genetic improvement in dry matter content in potato breeding, possibly reflecting differences in breeding objectives, germplasm base, and selection intensity between breeding programmes. This trend highlights the historical orientation of Indian potato breeding programmes toward improving yield, early maturity and late blight resistance, while total dry matter content (TDM) has received relatively less direct selection pressure and has largely been treated as a secondary quality attribute.

Considerable genetic variability in TDM exists among cultivated potato varieties (Johansen *et al.*, 1967; Ruttencutter *et al.*, 1979) reflecting its polygenic inheritance. Due to strong genotype environment interactions, multi-location evaluations are necessary for accurate selection. Quantitative trait loci (QTL) mapping has facilitated the identification of genomic regions associated with TDM and related traits like starch content. Several studies have reported allelic variants influencing tuber starch accumulation and quality (Li *et al.*, 2013; Schonhals *et al.*, 2016) and multiple QTLs associated with TDM have been mapped (Park *et al.*, 2021). However, the tetraploid nature of cultivated potato complicates marker-assisted selection (MAS) for TDM on account of its complex quantitative inheritance.

Genomic selection (GS) offers a more effective approach for improving TDM. Unlike MAS, GS utilizes genome-wide marker data to predict breeding values without the need to identify individual QTLs (Meuwissen *et al.*, 2001; Busse *et al.*, 2019). GS involves estimating genomic estimated breeding values (GEBVs) from a training population with known genotypic and phenotypic data, then using these GEBVs to select superior individuals in a test population based solely on genotypic information. This approach reduces breeding time and costs by minimizing field trials (Heffner *et al.*, 2010; Slater *et al.*, 2017). Prediction accuracies of 0.56 for starch content have been reported using cross-validation, which were observed to drop significantly in the range of 0.30–0.31 in independent test populations (Sverrisdóttir *et al.*, 2017, 2018). GS has also been successfully applied to predict traits such as chipping quality and starch content using genotyping by sequencing and statistical models (Endelman *et al.*, 2018; van Eck 2007; Li *et al.*, 2008; Fischer *et al.*, 2013; Schreiber *et al.*, 2014).

Exotic germplasm, including wild species and *Solanum tuberosum* ssp. Andigena, serves as a valuable source of genetic variation for enhancing TDM and incorporating resistance to traits like late blight. Chimote *et al.*, (2008) emphasized the value of such genetic resources in expanding the breeding base for high TDM varieties. Several studies related to TDM breeding have been summarized in Table 2.

The candidate gene approach has been widely used to explore genes involved in carbohydrate metabolism, starch biosynthesis and water regulation which are the key component characters determining TDM. Since starch constitutes the largest component of TDM, genes regulating starch biosynthesis are particularly important. ADP-glucose pyrophosphorylase (AGPase) catalyzes the first committed step in starch biosynthesis and plays a pivotal role in starch accumulation (Sun *et al.*, 2020). Starch branching enzymes (SBEs) have been reported to influence the architecture of amylopectin which affects starch quality and quantity (Yu *et al.*, 2021), while starch synthases contribute to the elongation of glucan chains during amylose and amylopectin synthesis (Nazarian-Firouzabadi and Visser 2017).

Genetic variations in several key biosynthetic genes including BMY-8/2 (a β-amylase gene), PHO1b (plastidic starch phosphorylase) and the large β-subunit of AGPase have been associated with differences in starch content and yield (Schreiber *et al.*, 2014). However, limited understanding of the regulatory mechanisms and enzymatic functions of these genes restricts their broader

Table 2. Genetic studies related to dry matter in potato

Freyre and Douches 1994	Diploid mapping population in three different locations and mapped ten putative QTL on chromosomes 1, 2, 3, 5, 7 and 1. Highest R2 QTLs explained 39-40% of variation
Schäfer-Pregl *et al.*, 1998	Eighteen Specific gravity QTL detected on all 12 potato chromosomes in segregating generations.
Li *et al.*, 2008	Loci linked to this trait on chromosomes 2, 3, 5, 7, 8, 9, 10 and 11 through candidate genes- or known loci-association mapping in tetraploid potato population
Li *et al.*, 2019	Specific gravity QTL on chromosomes 1, 2 and 8 after analyzing a Chinese tetraploid mapping population at three different locations for 2 years.
Schönhals *et al.*, 2016	The 450 genes observed to harbour markedly distinct SNPs and deemed primary functional candidates for regulating the inherent variability in tuber yield and starch content. 89 SNPs corresponding to 72 genes were proposed as primary targets for the development of diagnostic markers and breeding applications.
Park *et al.*, 2021	QTL analysis for russet family for tuber shape and TDM 11 significant QTL were reported specific gravity, appeared on chromosomes 1 and 5

application in breeding programs. This limits the practical utility of candidate gene based selection and transgenic approaches aimed at enhancing TDM in potato.

FUTURE PERSPECTIVES

Improvement of total dry matter (TDM) content in potato requires an integrated approach combining targeted breeding, advanced phenotyping, and alignment with evolving industry requirements. Future breeding efforts should prioritize the development of high-TDM genotypes with stable performance across diverse environments, while simultaneously maintaining high yield, early maturity, and resistance to major biotic and abiotic stresses. Broadening the genetic base through the incorporation of diploid germplasm, wild relatives, and pre-breeding populations will be critical to enhance genetic gain for TDM and processing quality traits.

Advances in phenotyping technologies, particularly non-destructive tools such as near-infrared spectroscopy (NIRS), hyperspectral imaging, and sensor-based high-throughput phenotyping platforms, offer significant potential to improve selection efficiency. These technologies enable rapid, accurate, and large-scale assessment of dry matter and related physiological traits, thereby accelerating breeding progress. Integration of phenomics with genomics-assisted breeding approaches, including marker-assisted and genomic selection, will further enhance the precision and efficiency of TDM improvement.

From an industry perspective, increasing demand for processing-grade potatoes necessitates the development of varieties with consistently high dry matter, low reducing sugars, and suitability for mechanized production and long-term storage. Future breeding programmes must therefore adopt a market-oriented approach, focusing on improving dry matter stability, processing quality, and adaptability to climate variability. Collectively, these efforts will be essential to meet the growing demand for high-quality potato raw material and ensure sustainable productivity and profitability across the value chain.

CONCLUSION

TDM is a fundamental quality parameter that affects the suitability of potato cultivars for diverse uses, including table consumption and industrial processing. The development of varieties with optimal TDM levels is therefore critical, especially for the processing industry where high TDM ensures improved frying quality, reduced oil uptake and enhanced end-product texture. Suitable choices for optimizing dry matter based on end use and consumer preference can be excised on account of genotype, planting region, elevation, soil type, harvesting dates, nutrient management etc. This offers immense opportunities for the stakeholders.

Higher tuber dry matter is directly linked to improved nutritional value and processing quality in potatoes. Globally, there is growing emphasis on breeding early-maturing potato varieties due to their environmental sustainability and their ability to evade various biotic and abiotic stresses compared to long-duration cultivars. Enhancing dry matter content in these early varieties is therefore crucial for enhancing both nutritional security and processing potential. Moreover, high tuber dry matter content is a fundamental requirement for processing grade potatoes as it directly influences product yield, texture, oil absorption and overall quality. With the rapid expansion of the potato processing industry driven by rising consumer demand for products, the ratio of processed to fresh potato use has increased significantly in recent years. This shift underscores the growing importance of developing varieties specifically tailored for processing, where elevated dry matter content not only enhances industrial efficiency but also aligns with economic and nutritional objectives.

This review emphasizes the various genetic, physiological, environmental and post-harvest factors that collectively influence TDM in potatoes. Multiple factors interact in a complex and interdependent manner to influence plant physiology and total dry matter (TDM) accumulation. These factors do not operate in isolation, rather their effects are integrative and synergistic, collectively determining the overall dry matter production and its partitioning within the plant. Consequently, no single factor can be identified independently as the sole determinant of TDM, as its accumulation is the outcome of the combined influence of genetic, physiological, and environmental components. To summarise among various traits, the duration and rate of tuber bulking, along with photosynthetic efficiency and assimilate partitioning efficiency (affected by the influencing factors), are the most critical determinants of total dry matter accumulation in potato. These traits directly regulate assimilate production, translocation, and storage in tubers, thereby exerting the strongest influence on final dry matter content.

A deeper understanding of the genetic control of TDM, including its polygenic inheritance and interactions with environmental variables, is crucial for accelerating the development of improved potato varieties. While traditional selection has yielded some progress, modern breeding approaches incorporating candidate gene analysis, quantitative trait locus (QTL) mapping and genomic selection offer new avenues for efficient cultivar development. Strategic selection of superior parental lines, integration of molecular tools and optimized agronomic practices can enable targeted improvement of TDM content. This integrated approach will ultimately benefit processors, consumers and producers by delivering cultivars with enhanced quality and market value.

Statements & Declarations

Authors certify by submitting a work to the journal that the submission is the authors' original study that has not been published elsewhere or is not currently under review by another journal.

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