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Impact of factors contributing to internal disorders of mango (*Mangifera indica* L.) fruit—A systematic literature review

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ABSTRACT

The expression of internal disorders is a complex phenomenon due to the interaction of genotype, environment, and management practices at the pre-harvest, harvest, and post-harvest stages. This study aims to provide a comprehensive overview of factors associated with, and have been investigated in relation to, the susceptibility and expression of internal disorders in mango. In this context, a systematic literature review was conducted to identify, extract, and analyse the most pertinent data. Six hundred and fifty-seven studies were sourced from three databases. Of these, 72 were relevant after screening based on exclusion-inclusion criteria. An additional nine relevant studies were identified through manual searches and included in the final data synthesis. From the 81 studies, the prevalent disorders were spongy tissue and jelly seed, followed by flesh browning and soft nose. 'Alphonso' expressed only spongy tissue disorder. By contrast, 'Tommy Atkins' simultaneously expressed multiple disorders, viz., soft nose, jelly seed, and stem-end cavity. Mineral composition of flesh and exposure to heat post-harvest (viz., sunlight, phytosanitary heat treatment, and elevated storage temperature) were prominent in association with IDs expression. Relatively high N, N/Ca, Mg/Ca, and K/Ca ratios and relatively low Ca and B were related to most disorders. With K and Mg, studies inconsistently suggested positive and inverse relationship with a particular disorder. While individual studies suggest casual relationships, there was a relative dearth of pre-harvest work on soil characteristics, growing conditions (e.g., temperature, rain, and VPD), crop physiology (e.g., age and biennial bearing) and management practices (e.g., fertilisation and irrigation) in the literature. This review provides a benchmark against which future research might adopt holistic approaches to contiguously ascertain predisposition of mango fruit to internal disorders across the pre-harvest, harvest, and post-harvest continuum.

1. Introduction

Mango (*Mangifera indica* L., family Anacardiaceae) is an economically important fruit crop grown in tropical and subtropical regions of Asia, Australia, Africa, and Latin America (Kiloes et al., 2022; Litz, 2009). Mango is known for its sweet taste, distinct aroma, and high carotenoid content (Sivakumar et al., 2011; Sivankalyani et al., 2016).

World mango production is increasing, for example, from 25 million tonnes in 2000 to over 57 million in 2021 (FAOSTAT, 2022). Furthermore, the volume of mango exports from 2000 to 2021 increased from 0.62 to 2.3 million tonnes, with an average annual increase of 26 % (FAOSTAT, 2022). This rise in global demand for mangoes presents challenges associated with fruit quality. For example, the internal quality of the fruit towards the end of the supply chain, particularly for export markets. Fruit internal quality is often compromised by internal physiological disorders, which frequently arise during pre-harvest fruit development and post-harvest storage (Mogollón et al., 2020; Raymond et al., 1998a; Raymond et al., 1998b). Such disorders lessen the internal quality of the fruit, potentially rendering it unsuitable for human consumption, and posing a problem for the mango industry (Ma et al., 2022).

In most of the world's major production areas, mango fruit are susceptible to various physiological disorders. They include spongy tissue, tip pulp, jelly seed, soft nose, insidious fruit rot, and taper tip disorders, to name a few (Andrade et al., 2022; Ma et al., 2022; Raymond et al., 1998a). Internal disorders (IDs) are not visible to the naked eye, making

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them nearly impossible to detect at early stages. Although IDs have been extensively studied in the literature, underlying mechanisms and causes are dynamic. A range of factors across pre-harvest, harvest, and post-harvest stages have been associated with expression of IDs (Léchaudel and Joas, 2007; Sivakumar et al., 2011).

This systematic literature review was conducted as a comparative comprehensive understanding of individual disorders affecting mango fruit quality and potential contributing factors. It aimed to identify gaps around interactions of pre-harvest, harvest, and post-harvest factors associated with fruit susceptibility to disorders and to better inform and facilitate future management of these disorders. It collates varying terminologies used to describe different and similar disorders based on symptoms or pictorial references towards a 'common language' for academic and industry sectors of the mango community. Strict inclusion criteria used in this review ensure that the published articles selection fits the study's objective and minimises literature biasness.

2. Methodology

Methodology utilised in this study followed the standard guidelines of systematic review outlined by the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Nightingale, 2009). The PRISMA workflow effectively shows information flow through different phases. A general workflow of PRISMA involves the following steps: (i) Scoping: formulating the study objectives and expected outcomes, (ii) Planning: developing a search strategy using specific terminologies and identifying suitable databases for the study, (iii) Identification: identifying and examining resulting papers, (iv) Screening and Eligibility: removing duplications, irrelevant titles, or abstracts and further elimination based on exclusion/inclusion criteria, (v) Data Extraction: extracting relevant data from selected papers in a structured format according to the study objectives, and (vi) Interpretation: providing a descriptive summary of the findings, interpretations, and limitations.

Three databases were selected for the initial search: ScienceDirect, Scopus and Web of Science. The search was conducted in November 2022. Search terms used for each database and the results are shown in Table 1. The search identified 657 potential papers for initial screening. The results were saved in RIS format and imported into the Covidence platform, an online screening and data extraction tool used for systematic review management (https://www.covidence.org/). Of the overall total considered, 123 papers were removed due to duplication across databases. A further 416 papers were excluded in the initial screening because the study title and/or abstract was not directly relevant to this study's objectives. During second phase screening, which involved full-text screening, 46 studies were excluded upon not meeting the inclusion criteria (Table 2). Additional searches were performed manually to identify and include papers that might have been missed from previous searches. Nine papers relevant to the study objectives were identified through manual search and subsequently included in the final set of papers for data extraction. The final result was 81 papers that included scientific articles, short communications, and conference papers, if sufficient information was available to meet requirements, in an inclusion timeline of 1971–2023 (Fig. 1).

For data extraction, each paper was read thoroughly and included in a structured extraction sheet coded as: Title, authors, study year, publication year, country of study, cultivar, publication type, study type, post-harvest treatments (if applicable), study length, fertiliser application (if applicable), type of disorder studied, and reason of defect (if applicable).

In the final step, the data was interpreted in a structured report consisting of a descriptive summary of the findings, interpretation of findings, discussion, and limitations. Disorders were classified through written or pictorial references of symptoms along with factors responsible for their expression in mango fruit. Descriptive figures were created by Microsoft Excel (365). 'Sankey' diagrams depicting association of IDs with cultivars and mineral concentrations were produced in R (4.0.2) using 'd3Network' package.

Thereafter, a causal loop diagram (CLD) was developed based on secondary data extracted from selected literature to discern nature of disorder expression in terms of multifactorial associations. CLD involves the extensive mapping of the feedback loops within a defined system (Haraldsson, 2004). IDs in mango were considered an output of a complex system and direct and indirect effects of various factors positively or negatively influencing the expression of IDs were mapped using Stella Architect systems modelling software considering its user-friendly interface and recognised iconography (Walters et al., 2016). Cause-and-effect relationships were represented between variables using arrows within the CLD. A positive sign (+) at arrowhead indicated a proportional relationship between cause and effect, and a negative sign (-) indicated an inverse relationship.

3. Descriptive analysis

In general, three types of publications were included for data extraction and analysis: scientific papers, short communications, and conference papers. Fig. 2 breakdowns number of publications over the past 5 decades, discussing one or more aspects of IDs. An increase in published studies was observed after 2000, which may have been associated with global increase in mango production and export (FAO, 2022; FAOSTAT, 2022). World mango export volume increased from 0.62 to 1.65 million tonnes over the 2000–2013 period (Evans et al., 2017). Such increase in export demand drives increase in quality control management as 'long' export supply chains often result in reduced shelf life, quality deterioration, and physiological disorders (Le et al., 2022). The highest number of publications ($n = 40$) discussing IDs of mango was conducted in India, followed by Brazil ($n = 13$), Spain ($n = 6$), China ($n = 3$), Philippines ($n = 3$), and USA ($n = 3$) (Fig. 3). When studies were categorised based on cultivar, 'Alphonso' was the most studied one for expression of IDs ($n = 29$), followed by 'Tommy Atkins' ($n = 12$), 'Keitt'

Table 1
Database searches by specific terminologies.

Database	Search terms	Results
ScienceDirect	("mango") and ("Internal disorders" OR "Internal breakdown" OR "physiological disorders" OR "internal browning" OR "jelly seed" OR "stem end cavity" OR "spongy tissue" OR "soft nose")	393
Scopus	(TITLE-ABS-KEY ("mango" OR "Mangifera indica") AND TITLE-ABS-KEY ("Internal disorders" OR "Internal breakdown" OR "flesh breakdown" OR "physiological disorders" OR "flesh browning" OR "internal browning" OR "jelly seed" OR "stem end cavity" OR "flesh cavity" OR "spongy tissue" OR "soft nose" OR "internal darkening"))	133
Web of Science	(TITLE-ABS-KEY ("mango" OR "Mangifera indica") AND TITLE-ABS-KEY ("Internal disorders" OR "Internal breakdown" OR "flesh breakdown" OR "physiological disorders" OR "flesh browning" OR "internal browning" OR "jelly seed" OR "stem end cavity" OR "flesh cavity" OR "spongy tissue" OR "soft nose" OR "internal darkening"))	131

Table 2
The exclusion and inclusion criteria for systematic literature review.

Criteria	Inclusion	Exclusion
Document type	Journal article Conference papers Short communications	Reviews Book chapters Thesis
Language	English	Non-English
Study objective	Discussing any aspect of internal disorders of mango	Not discussing internal disorders of mango
Full text	Available through web or library resources	Not available

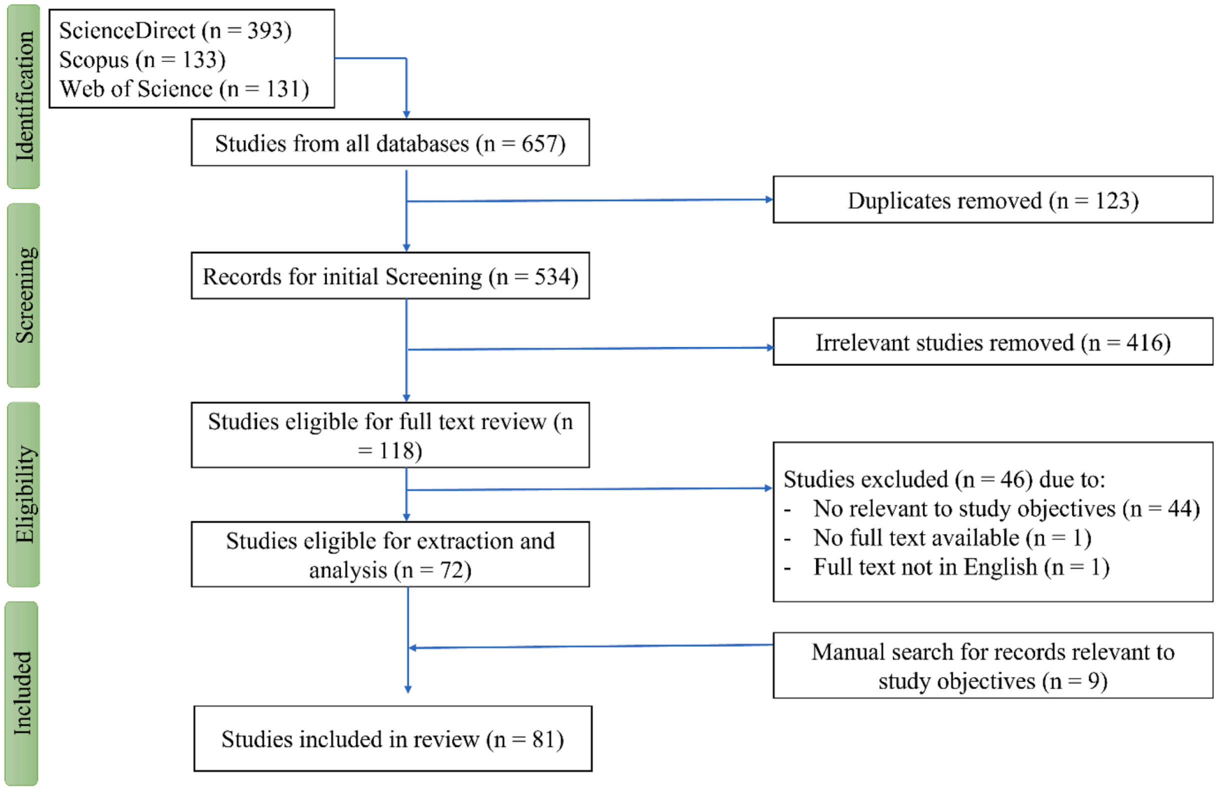

Fig. 1. Step-by-step literature selection process based on PRISMA flow diagram (Nightingale, 2009).

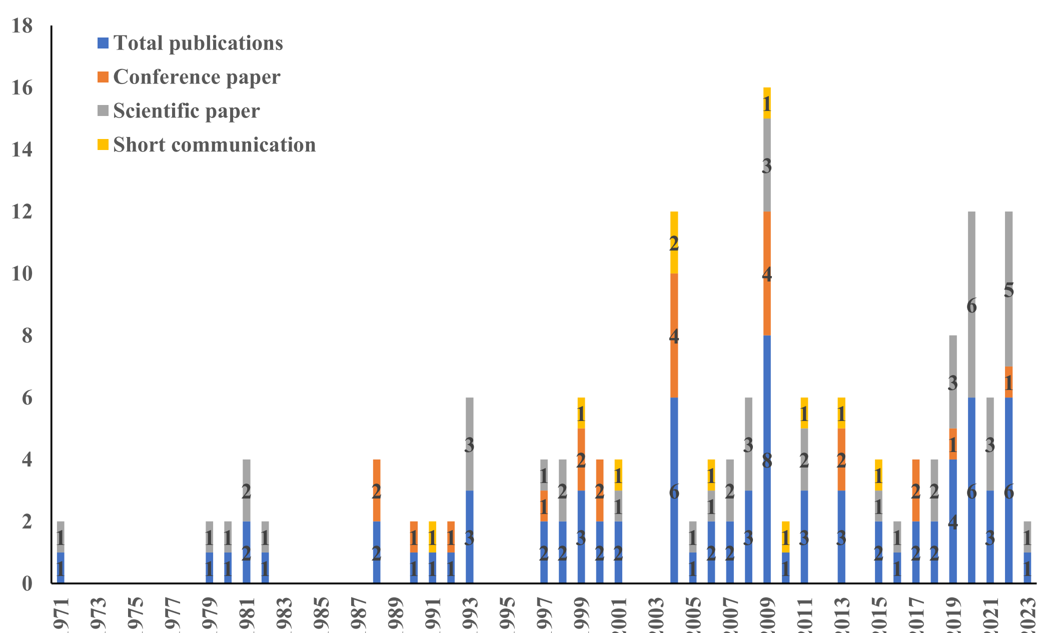

Fig. 2. Studies published over five decades discussing the IDs of mango.

($n = 10$), and 'Dashehari' ($n = 7$) (Fig. 4). Some studies discussed more than one cultivar for development of a particular disorder, e.g., Cracknell Torres et al. (2004) studied incidence of internal flesh breakdown in 28 different mango cultivars, and Srivastav et al. (2015) evaluated incidence of jelly seed disorder in 20 mango genotypes. Eleven publications highlighted incidence of IDs in 'not-so-popular cultivars' as represented by "other cultivars" in Fig. 4.

4. Internal disorders: Symptoms and classification

IDs in mango are also called flesh breakdown or internal physiological disorders. They are characterised by any disintegration/abnormality in fruit mesocarp that is non-pathogenic in nature (Wainwright and Burbage, 1989). Literature on mango IDs uses a range of specific or general terminologies to describe one or more types of defects. Table 3 presents a range of general and specific terminologies used in the

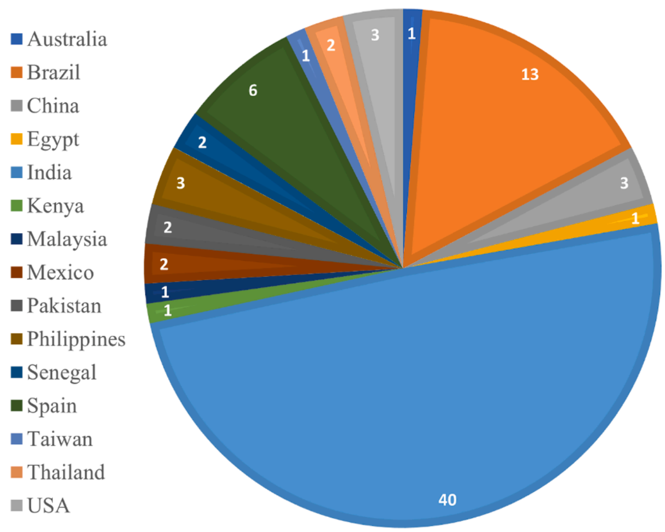

Fig. 3. Number of studies categorised based on country of study around the world.

literature and their manifestation as a disorder.

Specific terminologies are based on nature/appearance and/or location of the disorder within the mango fruit flesh. Soft nose is over softening and yellowing of fruit flesh at the distal end of the fruit (Fig. 5b) (Burdon et al., 1991; Raymond et al., 1998a). Spongy tissue is brown/yellowish/white corky spots and sponginess in the flesh with or without cavities or air pockets and off-odour (Fig. 5c) (Gunjate et al., 1979). Stem-end cavity is characterised by the presence of a cavity or air pocket in the fruit's proximal region in the mesocarp adjacent to the peduncle (Fig. 5d) (Raymond et al., 1998a). Jelly seed is associated with watery and jelly-like appearance of the mesocarp near and around fruit seed (Fig. 5e) (Andrade et al., 2022). Finally, flesh browning is characterised by brown/blackish discolouration of the fruit mesocarp around the seed (Fig. 5f).

However, the literature is rich with general terminologies, such that when symptoms are compared as to their written or pictorial reference, flesh browning is apparently also described as black flesh (Andrade et al., 2022; Mogollón et al., 2020), internal browning (Gabriëls et al., 2020), internal darkening (Acosta et al., 2000), internal necrosis (Saran and Kumar, 2011), and insidious fruit rot (Tarmizi et al., 1993). Another general terminology is internal breakdown/defects that collectively describe more than one type of disorder in individual fruit e.g., Raymond et al. (1998b) referred soft nose, stem-end cavity and jelly seed as generic term 'internal breakdown' in 'Tommy Atkins' mango.

Such discrepancies could create confusion when seeking an understanding of causal factors of IDs and their effective management. Soft nose was mostly attributed to mineral nutrient imbalance in the fruit flesh (Burdon et al., 1991, 1992), stem-end cavity was associated with fruit weight at harvest (Hermoso et al., 1997; Torres et al., 2009; Torres et al., 2004b), and flesh browning a response to post-harvest storage temperature and duration (Acosta et al., 2000; Pina et al., 2000) and to post-harvest heat treatment at the eating ripe stage (Jabbar et al., 2011) (Fig. 7). Moreover, some cultivars are more susceptible to a specific disorder expression than are others. For instance, 'Alphonso' and 'Dashehari' are highly susceptible to spongy tissue and jelly seed respectively, and 'Sensation' is prone to stem-end cavity and spongy tissue disorders (Fig. 7). 'Beverly', 'Kent', and 'Chauns' are susceptible to soft nose. 'Keitt' and 'Tommy Atkins' express almost all disorders, viz., soft nose, jelly seed, spongy tissue, flesh browning and stem-end cavity (Fig. 7). Major contributing factors in the expression of internal disorders

Contributing factors associated with the expression of IDs in mango fruit in selected literature are shown in Fig. 6. Mineral nutrient imbalance in terms of access and/or deficiency was the dominant factor in disorder expression ($n = 22$). Other factors were post-harvest temperature management, including the storage temperature ($n = 5$), post-harvest quarantine heat treatment ($n = 4$) and sun exposure after harvest in the field ($n = 3$). Some studies mention multiple reasons in single publications for expression of IDs in single publication. For example, Esguerra et al. (1990) asserted fruit maturity and post-harvest vapour heat treatment as being collectively responsible for spongy tissue in

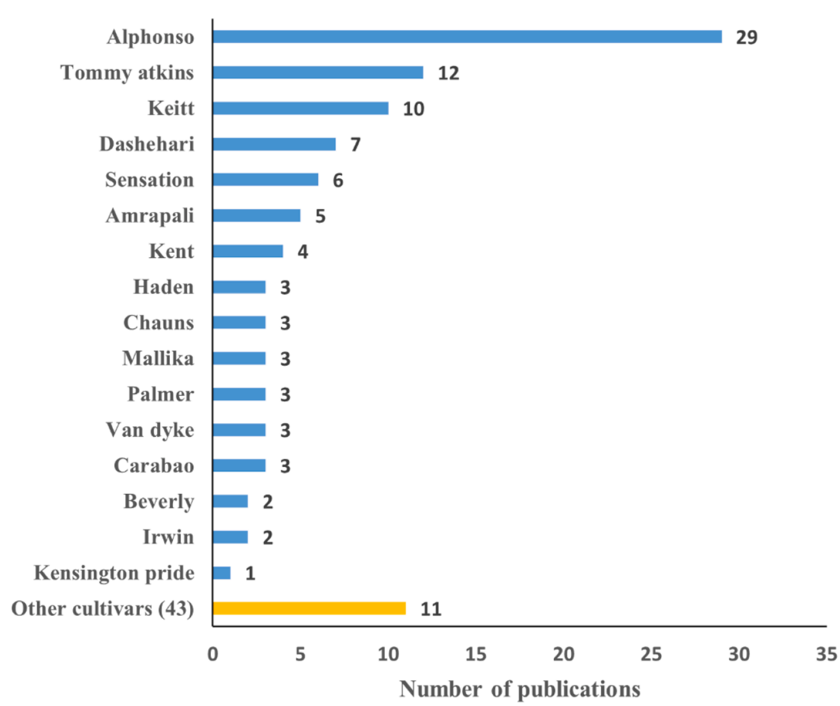

Fig. 4. Number of studies discussing the IDs in major mango cultivars over five decades. Some studies discussed more than one cultivar for single or multiple disorders within a single publication.

Table 3
General and specific terminologies and symptoms as mentioned in the literature to describe different IDs of mango.

General terminologies	Specific terminology	Symptoms	Similarity	References
—-	Spongy tissue	Brown/yellowish/white corky patches with or without air pockets/cavities and sponginess in flesh	—-	(Andrade et al., 2022; Burondkar et al., 2009; De Oliveira Lima et al., 1999; Gunjate et al., 1979; Gunjate et al., 1982; Janave, 2009; Janave and Sharma, 2008; Katrodia and Rane, 1988; Katrodia and Sheth, 1988; Krishnamurthy, 1980; Lima et al., 2001; Ma et al., 2023; Mehta et al., 2013; Nagamani et al., 2010; Oak et al., 2019; Oak et al., 2022; Raja, 2009; Ravindra and Shivashankar, 2004, 2006; Ravindra et al., 2010; Shinde et al., 2006; Shinde et al., 2009; Shivashankar et al., 2007; Shivashankar and Sumathi, 2019; Shivashankar et al., 2015; Shivashankara and Mathai, 1999; Singh et al., 2006a; Thomas et al., 1993; Torres et al., 2004b; Vasanthaiah et al., 2008; Vasanthaiah et al., 2006)
—-	Jelly seed	Deeper yellow-orange colour/ watery and jelly appearance of the mesocarp tissue	—-	(Andrade et al., 2022; Bitange et al., 2020; Krishna et al., 2020; Krishna et al., 2019; Lin et al., 2013; Mogollón et al., 2020; Raymond et al., 1998a; Seshadri et al., 2019; Shivashankar et al., 2016; Srivastav et al., 2015; Torres et al., 2009; Torres et al., 2004b; Whangchai et al., 2001)
—-	Soft nose	Over softening/breakdown of flesh near distal end	—-	(Amin et al., 2007; Burdon et al., 1991, 1992; Jabbar et al., 2011; Lin et al., 2013; Raymond et al., 1998a)
—-	Stem-end cavity	Cavity and discolouration at stem-end in the flesh	—-	(Hermoso et al., 1997; Raymond et al., 1998a; Torres et al., 2009; Torres et al., 2004b)
Internal breakdown/ flesh breakdown/ Internal necrosis	—-	Pale yellow/white flesh with air pockets/ cavities	Spongy tissue	(Bizzani et al., 2020; Esguerra et al., 1990; Hermoso et al., 1997; Hofman et al., 1997; Kitma and Esguerra, 2009; Lizada and Rumbaoa, 2017; Ma et al., 2022; Ma et al., 2018; Subraman et al., 1971)
		Brown-black flesh and flesh discolouration	Flesh browning	(Bizzani et al., 2020; Ma et al., 2022; Saran and Kumar, 2011; Seehanam et al., 2022)
		Tissue collapse and watery areas	Jelly seed	(Oldoni et al., 2022)
Internal browning/ darkening/ discolouration/ black flesh	—-	Browning in the mesocarp of fruit	Flesh browning	(Acosta et al., 2000; Andrade et al., 2022; Gabriels et al., 2019; Gabriëls et al., 2020; Jabbar et al., 2011; Lo'ay and Ameer, 2019; Mogollón et al., 2020; Pina et al., 2000; Tarmizi et al., 1993)

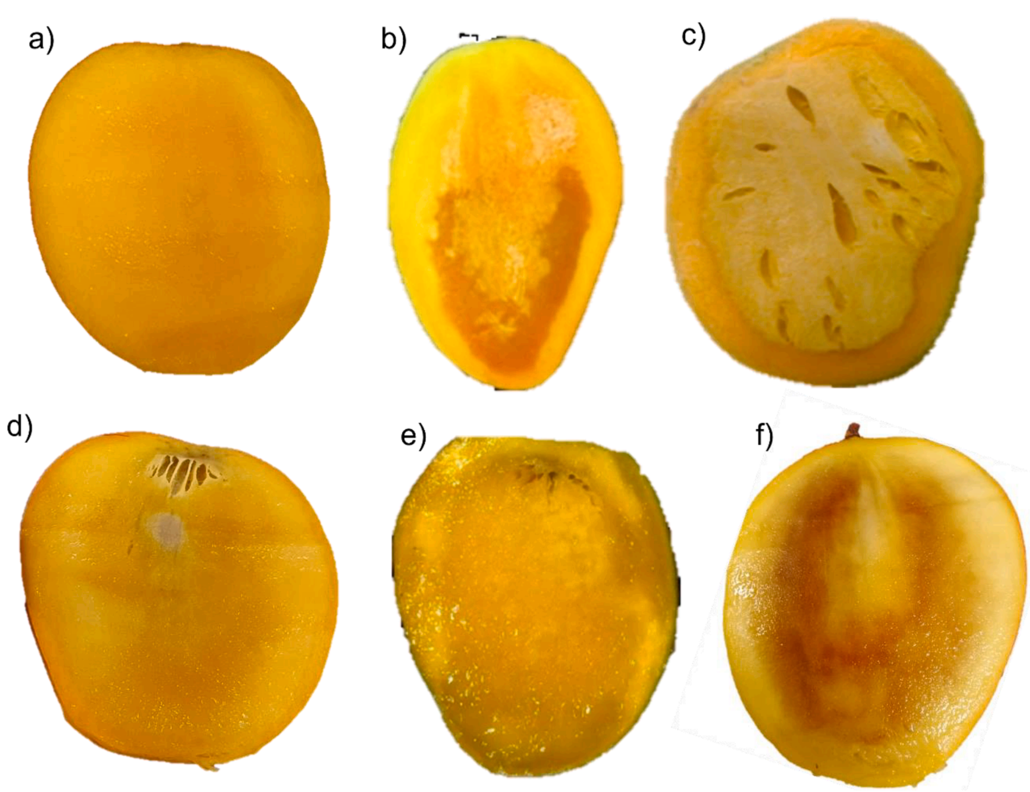

Fig. 5. Internal disorders of mango. a. No disorder (control), b. Soft nose disorder (Lin et al., 2013), c. Spongy tissue disorder (Oak et al., 2019), d. Stem-end cavity disorder (Asad et al. unpublished), e. Jelly seed disorder (Andrade et al., 2022), and f. Flesh browning disorder (Asad et al. unpublished).

'Carabao' mango. Similarly, Raja (2009) considered pre-harvest high temperatures and humidity and mineral nutrient imbalance in the leaves as potential contributing factors to spongy tissue disorder in 'Alphonso' mango. A number of studies in the selected literature (n = 31) had focused mainly on molecular and biochemical aspects and/or non-destructive detection of IDs (Mogollón et al., 2020; Oak et al., 2019;

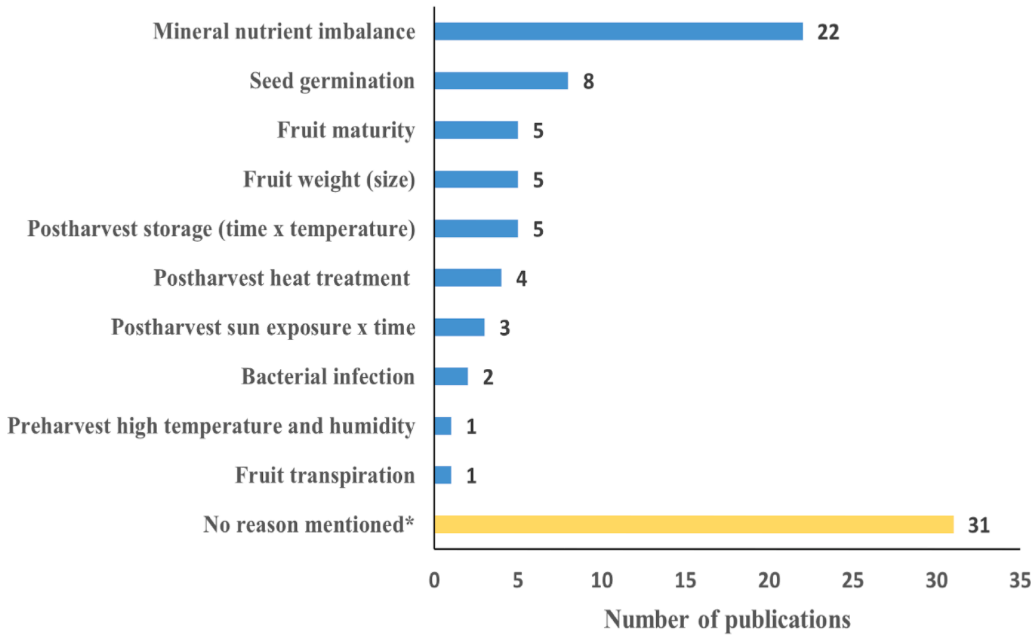

Fig. 6. Breakdown of factors discussed in selected literature for expression of mango IDs. '*' denotes studies discussing molecular, biochemical aspects, and non-destructive detection of IDs.

Oak et al., 2022; Raymond et al., 1998a; Thomas et al., 1993). These did not identify nor discuss a factor, *per se*. Spongy tissue was associated directly and/or indirectly with all of the factors discussed in the literature (Fig. 7). However, jelly seed was only linked to mineral nutrient imbalance in the fruit flesh, fruit weight at harvest, and premature seed germination (Andrade et al., 2022; Shivashankar et al., 2016; Singh and Swati, 2011; Torres et al., 2009; Torres et al., 2004b) (Fig. 7). The role of each contributing factor is discussed in detail in the following sections.

4.1. Mineral nutrients

One of the most important and well-discussed contributing factors in

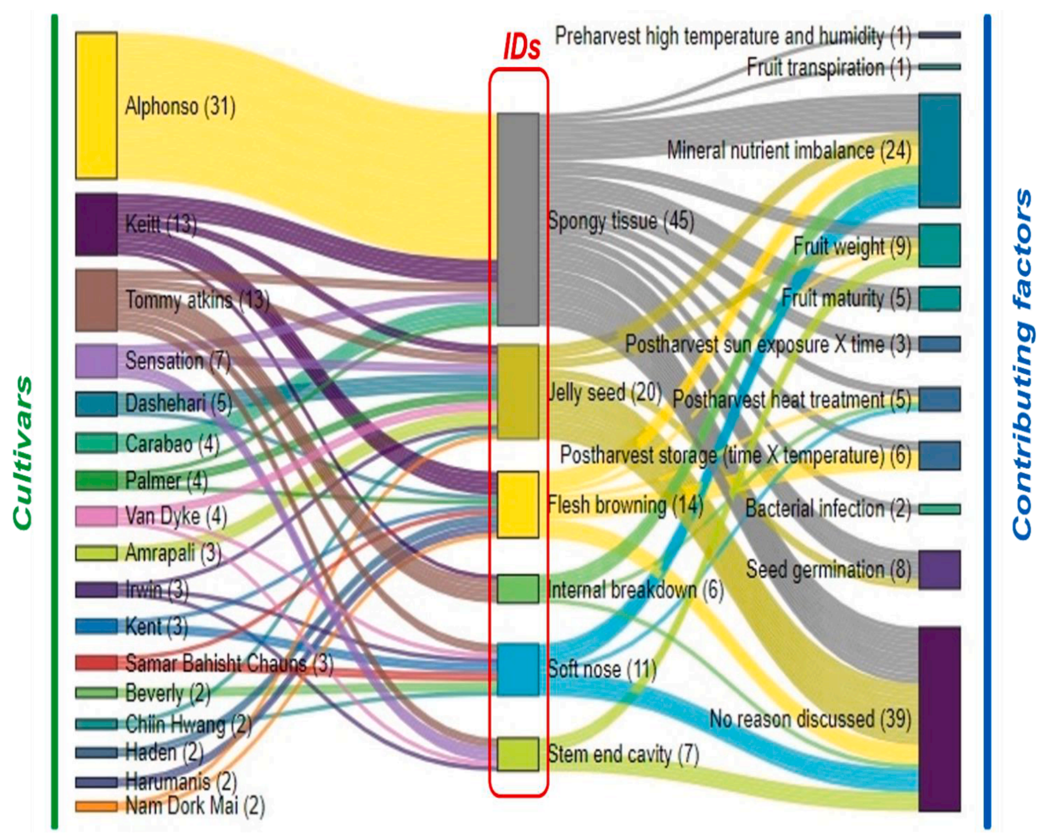

Fig. 7. Classification and association of cultivar vs. IDs and respective contributing factors in the selected literature. Herein, the term 'internal breakdown' refers to presence of multiple disorders all at once in single fruit, i.e., soft nose, jelly seed, stem-end cavity, and/or flesh browning.

literature to mango fruit ID expression is mineral nutrient imbalance, either deficiency or access ($n = 22$) (Figs. 6 and 7). Mangoes require a range of nutrients to grow and develop properly (Bally, 2009). Obtaining an optimum balance of mineral nutrients is likewise important to define fruit quality, in the context of varying genetic, management, and environmental influences at pre-harvest fruit development and post-harvest handling stages (Bally, 2009; Léchaudel and Joas, 2007).

Ca deficiency is the mineral most studied and associated with expression of IDs in mango. Ca deficiency has been linked to spongy tissue in 'Alphonso' (Gunjate et al., 1979; Raja, 2009; Subraman et al., 1971) and 'Keitt' (Andrade et al., 2022; Ma et al., 2023; Ma et al., 2022; Ma et al., 2018), flesh browning (Andrade et al., 2022; Tarmizi et al., 1993), soft nose (Burdon et al., 1991, 1992), and jelly seed (Andrade et al., 2022; Bitange et al., 2020; Singh and Swati, 2011) (Fig. 8, Table S1). Ca, as Ca^{2+}, provides membrane stability and cell wall strength through cross-linkages of pectin and carboxylic groups (Hocking et al., 2016). Therefore, Ca deficiency weakens the cell wall and renders fruit susceptible to breakdown during post-harvest rigours and stresses (Tonetto de Freitas and Mitcham, 2012). Ca concentrations in fruit flesh depends on fruit growth rate and transpiration (Hocking et al., 2016). Fruit transpires at relatively high rates per unit fresh mass at early developmental stages, particularly during rapid cell division. They thus accumulate much of their Ca during early growth phase (Joyce et al., 2001; Montanaro et al., 2010). As fruit develop and mature, they enter the predominantly cell expansion stage and Ca intake decreases drastically (Joyce et al., 2001; Montanaro et al., 2010). This decline in Ca at later stages is attributed to reduction in xylem sap uptake due to the loss of xylem functionality and hydrostatic gradient between fruit and pedicel, generated by fruit growth and transpiration (Nordey et al., 2015). Transpiration is restricted at later stages as functional stomata turns into lenticels and the formation of thick cuticle wax on mango fruit surface (Bally, 1999). Therefore, adequate availability of Ca during critical early growth stages may make a major difference in overall fruit Ca concentrations and post-harvest quality.

Boron (B) deficiency was associated with browning and cracking-like symptoms in mango fruit flesh (Saran and Kumar, 2011), along with spongy-like cavity formation in 'Keitt' (Ma et al., 2018). Plants uptake B as either boric acid (H_3BO_3) or borate ions (BO_3^-) and is important for fruit set by regulating pollen tube growth, pollen germination, and flower development (Bally, 2009). Saran and Kumar (2011) reported significantly ($p \leq 0.05$) lower levels of B in fruit flesh expressing flesh browning symptoms in 'Dashehari' mango fruit. Foliar application of B as disodium octaborate tetrahydrate was effective in improving B levels, yield and reducing disorder.

Relatively high concentrations of N and phosphorus (P) were associated with mango fruit expressing a number of IDs (Andrade et al., 2022; Burdon et al., 1991; Ma et al., 2023; Subraman et al., 1971; Torres et al., 2004a). N is acquired as NH_4^+ and/or NO_3^- and tends to stimulate vegetative growth and increase fruit set, retention, and weight (Bally, 2009; Ibell et al., 2017; Nguyen et al., 2004). Untimely application of N may stimulate new growth flush during early fruit developmental stages, consequently redirecting Ca influx from fruit towards young leaves with high transpiration rates. P, on the other hand, is present as plant available $H_2PO_4^-$ and/or HPO_4^{2-} ions and involved in root tip elongation, cell division and growth and, is an essential component of sugar phosphates that regulate respiratory and other cellular energy metabolism

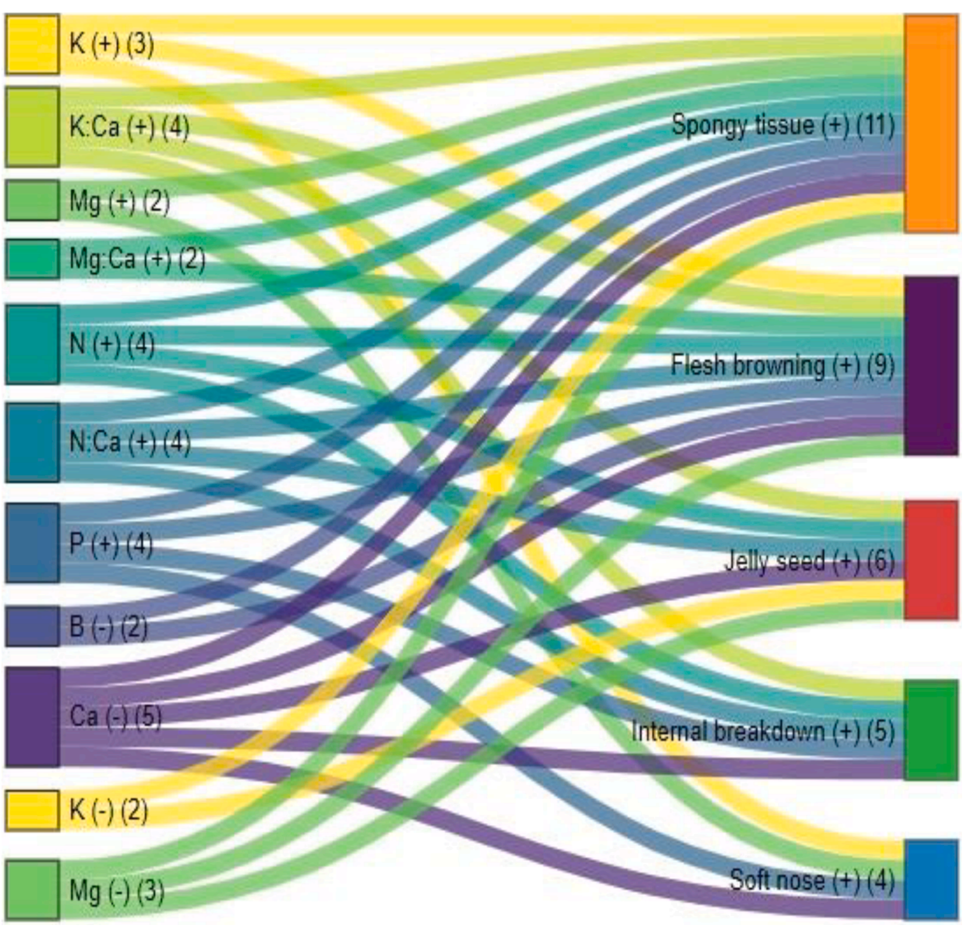

Fig. 8. Association of the individual mineral element in mango flesh and their ratios with the expression of internal disorders. '+' sign in disorder column indicates an increase in disorder with an increase (+) and decrease (-) in mineral element concentrations in mango flesh. Here, the internal breakdown term refers to the expression of the combination of soft nose, jelly seed and stem-end cavity disorder in single fruit at once. For detailed information on individual studies, see Table S1.

mechanisms (Bally, 2009).

The influences of mineral nutrition can be modulated by G x E x M. 'Keitt' mango from Brazil had Ca concentrations of 1000 mg/kg D.W. in healthy and ~200 mg/kg D.W. in spongy tissue-affected fruit (Andrade et al., 2022). Ma et al. (2023) reported Ca concentrations of ~175 mg/kg D.W. in healthy and ~125 mg/kg D.W. in spongy tissue affected 'Keitt' fruit grown in China (values were estimated from graphs). There were conflicting reports of magnesium (Mg) and potassium (K) in terms of their associated with spongy tissue disorders (Fig. 8, Table S1). For example, Andrade et al. (2022) reported [Mg] deficiency and Ma et al. (2023) reported [Mg] excess in spongy tissue-affected 'Keitt' mango from Brazil and China, respectively. Reasons for such discrepancies in the literature are elusive and make it impractical to name optimum nutrient levels for robust fruit. However, mineral nutrient ratios, like N/Ca, K/Ca, and Mg/Ca, may be more reliable indicators of ID susceptibility in mango. There has been a consistent trend of higher ratios of these minerals in fruit affected with internal disorders compared to healthy fruit (Andrade et al., 2022; Ma et al., 2023; Ma et al., 2022; Tarmizi et al., 1993). Nevertheless, and as for individual element concentrations, specific ratios are elusive. Hence, predicting fruit quality based on mineral nutrient concentrations and ratios may need to be optimised for genotype, environment, and management practices.

4.2. Temperature exposure

Temperature regulates critical development processes, including growth, maturation, and ripening, and mediates post-harvest product quality and shelf life (Fonseca et al., 2002; Paull and Chen, 2000). Raja (2009) reported a marked increase in spongy tissue in 'Alphonso' mango in humid climate (humidity: 60–70 %, rainfall: 2500 mm/year) with higher growing temperatures compared to a semi-arid climate (humidity: 25–30 %, rainfall: 650 mm/year). Pre-harvest temperatures modulate developmental aspects of mango fruit physiology through transpiration rate and water loss that determines nutrient movement, diurnal shrinkage, growth rate, and ultimately fruit quality and susceptibility to IDs (Montanaro et al., 2006; Shivashankara and Mathai, 1999; Singh et al., 2006b). Influences of temperature on the development of important quality traits, such as fruit size, taste, and aroma are well documented (Génard and Bruchou, 1992; Hewett, 2006).

Post-harvest temperature management includes limited exposure to field temperatures and sunlight at harvest, post-harvest phytosanitary heat treatments as a control measure for fruit fly infestation for export, and low-temperature storage in transit (Acosta et al., 2000; Esguerra et al., 1990; Gunjate et al., 1982) (Fig. 7). Mango fruit exposed to heat after harvest can alter its physiology such as to hinder normal physiological processes and ripening (Gunjate et al., 1982; Katrodia and Sheth, 1988). Studies in the 1980s highlighted the critical roles that sunlight and field temperatures play in the development of IDs in mango. Gunjate et al. (1982) exposed harvested 'Alphonso' mango to a direct sunlight-induced internal fruit temperature range of 37.5–49°C for 5–240 min and observed a linear increase of the incidence of spongy tissue disorder from 10 % to 100 % in control (no exposure) to 240 min sunlight exposed fruit. Similarly, the sun-exposed side with internal temperature of 43.8°C of an 'Alphonso' mango manifested 100 % spongy tissue disorder incidence as compared to 0 % for the unexposed side (39.2°C) (Katrodia and Sheth, 1988). Such studies paved the way for early management guidelines to limit direct sunlight exposure and to precool at the earliest convenience after harvest.

Post-harvest phytosanitary heat treatments, like vapour heat treatment (VHT) and hot water treatment (HWT), are important for mango exports to specific protocol countries as a quarantine treatment for fruit fly and other pests, like mango seed weevil. In post-harvest heat treatments, the fruit mesocarp temperature is raised to 47°C and maintained for 15 min by hot moist air (VHT) or hot water dips (HWT) (Jacobi et al., 2001). Temperature range and duration can vary depending upon a cultivar's susceptibility to heat injury. Both treatments kill fruit fly eggs and larvae, but can induce disorders depending upon the cultivar and inherent fruit robustness (Esguerra et al., 1990; Kitma and Esguerra, 2009). Jabbar et al. (2011) reported internal discolouration (flesh browning) and soft nose disorder in HW-treated 'Chauns' mango. Esguerra et al. (1990) sorted fruit based on maturity using 1 % salt solution and observed white starchy lesions, termed spongy tissue, in immature (floaters) 'Carabao' mango fruit subjected to VHT. Kitma and Esguerra (2009) reported a similar disorder in 'Carabao' mango upon HWT treatment. However, conditioning the fruit using hot air prior to HWT significantly ($p \leq 0.05$) reduced the incidence of white starchy lesions or spongy tissue disorder. Since phytosanitary treatments are essential for mango export to protocol countries, appropriate measures (e.g., resilient maturity stage, conditioning) to ensure that fruit remain free of IDs that otherwise would be revealed at the consumer's end of the supply chain.

Post-harvest storage and transport, including time and temperature, is also pivotal in maintaining fruit quality throughout the supply chain, especially for longer, in terms of time and/or distance, export supply chains. Prolonged periods of storage at low temperatures and/or in modified atmosphere packaging can lead to internal hypoxia (oxygen starvation) precipitating mesocarp degradation, internal breakdown, and browning (Lizada and Rumbaoa, 2017; Pina et al., 2000). Acosta et al. (2000) reported that the incidence of internal darkening (flesh browning) increased from 6 to 78 % and 56 to 94 % with an increase in storage duration from 22 to 28 days at 13°C and 18°C, respectively, in 'Haden' mango. Fruit stored at 8°C didn't show any such symptoms until day-26 but did suffer low temperature-induced chilling injury after 24 days storage.

Incidence of IDs can be minimised by limiting sun exposure, choosing appropriately mature fruit for post-harvest heat treatment, and maintaining a balance in storage time and temperature with respect to cultivar so as to preserve the quality and longevity of mango fruit (Wills and Golding, 2016b).

4.3. Fruit characteristics (size, maturity)

Fruit characteristics such as maturity and weight at harvest are essential to meet consumers' preferences, and can markedly alter post-harvest fruit physiology, quality and shelf life (Wills and Golding, 2016a).

Mango fruit are usually harvested at the hard green mature stage before the onset of the climacteric respiration rise (Hofman and Whiley, 2010). Immature and overmature fruit tend to develop poor texture, flavour, and aroma. While early harvest immature fruit exhibit longer shelf life, they tend to express disorders upon post-harvest heat treatments (Esguerra et al., 1990; Jacobi et al., 2001). On the other hand, overmature fruit have shorter shelf life but are also more susceptible to express disorders (Bally, 2006). Subraman et al. (1971) and Burondkar et al. (2009) reported a higher incidence of spongy tissue in middle-to-late harvested 'Alphonso' mango compared to early harvest. The 'Alphonso' mango were sorted into three maturity classes based on specific gravity, viz., < 1.00, 1.00–1.02, and > 1.02 (Krishnamurthy, 1980, 1982). The percent incidence of spongy tissue was 4 % in <1.00 specific gravity fruit compared to 33 % and 63 % in 1.00-1.02 and >1.02 respectively, indicating higher susceptibility in more mature fruit.

Fruit weight is another particularly important characteristic of mango fruit. Along with external appearance (e.g., colour, blemish), weight is most often used as an index for fruit grading category for target domestic and/or export markets. The relationship between mango fruit size and susceptibility to IDs depends on the cultivar and type of disorder. For example, Subraman et al. (1971) reported that an increase in fruit weight from > 200 to > 300 g significantly ($p = 0.1$) increased the spongy tissue disorder in 'Alphonso' mango from 18.2 % to 44.5 %, respectively. A similar trend was noted for 'Harumanis' mango for insidious fruit rot (flesh browning) disorder, with fruit having < 350 g weight had 7.4 % and 451–500 g fruit had 35.1 % incidence of disorder

(Tarmizi et al., 1993). Also, jelly seed disorder was noted to be positively correlated with fruit size in N-fertilised experimental trees, but not in unfertilised control trees (Torres et al., 2009; Torres et al., 2004b).

Contradictory reports were noted in 'Sensation' mango between stem-end cavity disorder and fruit weight (Hermoso et al., 1997; Torres et al., 2009; Torres et al., 2004b). Hermoso et al. (1997) found negative correlation and Torres et al. (2009) reported positive correlation between fruit weight with stem end cavity disorder in 'Sensation' mango. However, in later studies (Torres et al., 2009; Torres et al., 2004b), 'Sensation' trees were heavily N fertilised with biennial/alternate crop bearing pattern for the entire duration of experiment which can most likely influence fruit characteristics and incidence of IDs respectively. Thus, it is very difficult to separate whether the incidence of stem-end cavity disorder was entirely due to fruit weight or if crop load and/or N fertilisers also contributed to fruit's susceptibility during development and maturation.

4.4. Premature seed germination

Premature seed germination causing IDs was first explored in the Indian cultivars 'Alphonso' and 'Amrapali' for spongy tissue and jelly seed disorders, respectively (Ravindra and Shivashankar, 2004; Shivashankar et al., 2016).

Comparative physiological, biochemical, and mineral analysis indicated that seeds of spongy tissue-affected 'Alphonso' mango fruit had higher respiration rates, higher amylase, and lipase activities, moisture, and greater Ca concentrations compared to seeds in healthy fruit (Ravindra and Shivashankar, 2004). The results implied that withdrawal and remobilization of minerals and water from fruit mesocarp into the seed caused spongy tissue symptoms (Ravindra and Shivashankar, 2004, 2006; Ravindra et al., 2010). The early onset signs of spongy tissue were linked to a burst of ethylene production and an increase in cytokinin and gibberellins in seed that signalled the onset of germination (Shivashankar and Sumathi, 2019; Shivashankar et al., 2015).

Pre-harvest application of paclobutrazol markedly reduced the incidence of spongy tissue and jelly seed in 'Alphonso' and 'Amrapali' mangoes, respectively (Ravindra et al., 2010; Shivashankar et al., 2007; Shivashankar et al., 2016). This was interpreted to be by downregulating seed metabolism and amylase activity. In contrast, gibberellic acid aggravated the disorders upon upregulating general metabolic and amylase activity (Ravindra et al., 2010; Shivashankar et al., 2007; Shivashankar et al., 2016). Seshadri et al. (2019) recommended a pre-harvest spray of a salt formulation that primarily consisted of NaCl, $CaCl_2$, KCl, and low concentrations of H_3BO_3, $CuSO_4$, $ZnSO_4$, $FeSO_4$, $MnSO_4$, and EDTA as an effective preventive measure for jelly seed in 'Amrapali'. This formulation delayed seed germination by eliciting abscisic acid and germination-inhibiting phenolics in the seed with reduced jelly seed disorder (Seshadri et al., 2019).

4.5. Bacterial infection

In Fig. 6, two studies in the selected literature noted the presence of gram-positive *Staphylococcus xylosus* bacteria as a potential causative factor for spongy tissue disorder in 'Alphonso' mango (Janave, 2009; Janave and Sharma, 2008). Previous work by Subraman et al. (1971) on spongy tissue-affected 'Alphonso' had not given any clear indication of the presence of a pathogen and its role as the primary causative agent of internal disorder. They discussed isolation of *Bacillus sp.* from disordered tissue but did not establish pathogenicity. Hence, further investigations are required to corroborate this prospect.

5. Interacting factors influencing expression of internal disorders

From above, it is evident that expression of IDs is intricate due to multiple positive and negative predisposing interacting factors across pre-harvest, harvest, and post-harvest stages (Fig. 9). The majority of aforementioned studies in the selected literature highlight one to a few causal factors.

Accordingly, characterising the complex interplay of individual factor effects on IDs of mango is challenging, including because of interactions across the dynamic G x E x M continuum.

A first step in managing fruit susceptibility to IDs is perhaps to recognise that the interactive relationships may be overlooked during reductive scientific practice. A second may be recognising pre-harvest fruit growth and development and postharvest ripening and senescence as a dynamic continuum.

The majority of relevant literature identified in the course of this systematic literature review focused on fruit minerals concentrations and their association with IDs and typically recommended fertiliser applications to improve fruit nutrient levels (Andrade et al., 2022; Krishnamurthy, 1982; Ma et al., 2023; Ma et al., 2022; Shinde et al., 2006; Shinde et al., 2009; Tarmizi et al., 1993; Torres et al., 2004a). However, efficacy needs to account for factors that mediate nutrient uptake from the growth substrate and transport through the tree and into the fruit (Gilliham et al., 2011; Hocking et al., 2016; Tonetto de Freitas and Mitcham, 2012). These deterministic variables include soil properties, like pH, moisture, and nutrient holding capacity (Jackson and Meetei, 2018; Marschner and Rengel, 2023), root properties, like morphology, distribution, and health (Mengel, 1995), tree properties, like canopy volume, fruit set, and crop load (Bally, 2006; Isarangkoo et al., 2019; Robinson and Lopez, 2010; Serra et al., 2016; Zabedah et al., 2008), and environmental conditions, like temperature, VPD and rainfall (Gunjate et al., 1982; Ho and Adams, 1994; Montanaro et al., 2006). Moreover, all such factors change constantly with time across any one crop cycle, affecting the flowering, fruit set and development cycle and fruit characteristics at harvest, like size, maturity, and robustness (Léchaudel and Joas, 2007).

Considering this complexity, a causal loop diagram is proposed to organise and help understand the interplay of factors affecting fruit qualities at harvest and attendant postharvest susceptibility to disorders (Fig. 9). The prototype association of deterministic variables is presented with arrowheads having positive and negative signs indicating direct and inverse relationships, respectively. Pre-harvest factors suggest monitoring temperature, rainfall and VPD during fruit set and development stages, also taking appropriate management decisions (e.g., fertiliser application, irrigation scheduling, canopy pruning) into account. For example, to maintain optimum soil moisture levels for nutrient availability in the soil and root health for uptake via feeder roots. In this regard, an ideal rootstock-scion combination can improve nutrient uptake and distribution in the tree (Iyer and Subramanyam, 1992; Iyer and Degani, 1997). Dynamic interactions of environmental conditions and management practices needs to be understood and ideally monitored and managed on a seasonal basis to ensure consistency of fruit quality.

Likewise, fruit physicochemical attributes such as weight and maturity, are important factors determining a fruit's susceptibility to IDs (Hermoso et al., 1997; Krishnamurthy, 1980). However, the timeline is dynamic across pre-harvest through harvest into postharvest, with pressures associated with fruit treatment, handling, and distribution, like for domestic versus overseas markets. For instance, fruit harvested at higher maturity tend to have greater incidence of spongy tissue (Krishnamurthy, 1980) or, where post-harvest VHT treatment is involved, the less mature fruit may be more likely to develop spongy tissue disorder (Esguerra et al., 1990) (Fig. 9). Towards understanding how fruit are likely to behave, it is instructive to consider what stresses it may endure in the supply chain, including phytosanitary treatments (VHT, HWT, irradiation) and low-temperature storage conditions and durations, including for relatively long export supply chains. Conceptual comprehension of entire farm orchard to retail store systems, as facilitated by CLDs should inform the production of relatively more robust fruit through enlightened management of factors otherwise likely to

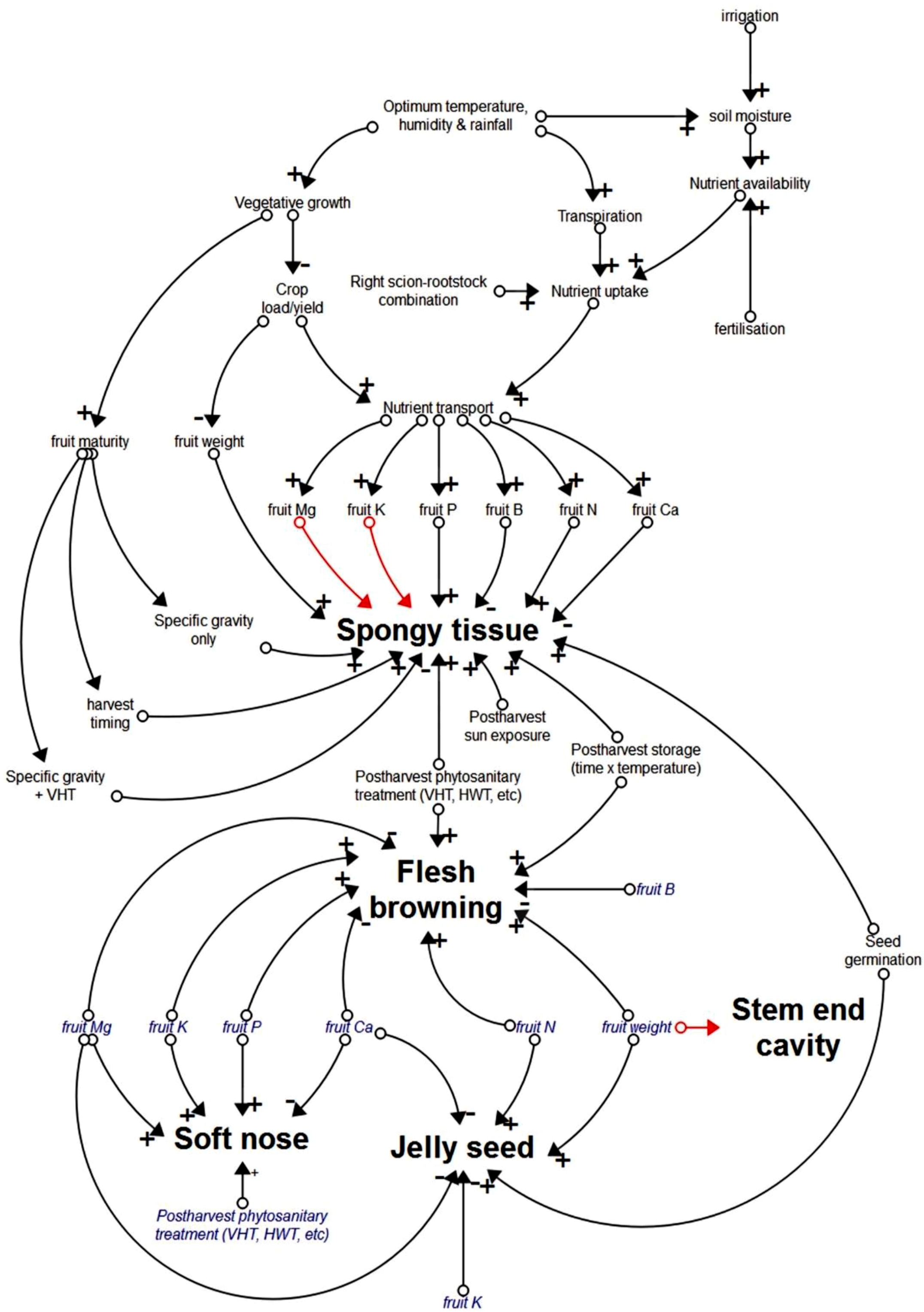

Fig. 9. A notional high-level causal loop diagram (CLD) encompassing pre-harvest, harvest, and post-harvest factors associated with G x E x M practices in the context of predisposition to expression of various internal disorders in mango fruit flesh. '+' and '-'on arrowheads indicate positive or negative effects, respectively, on subsequent factors in loops. '±' effects were indicated with the red coloured arrows. Blue italicised variables are 'shadow variables' of the original variables presented as such to avoid overlapping arrows. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

increase the incidence of IDs.

6. Conclusion

The current study systematically reviews progression of research on underlying causes of internal physiological fruit disorders in mango cultivars. From systematic literature review, mineral nutrition imbalance in fruit flesh was the single most studied factor, along with fruit size and maturity characteristics at harvest, and post-harvest management practices that include storage conditions and phytosanitary treatments. The analysis suggests that these variables directly and/or indirectly profoundly influence mango fruit quality in terms of susceptibility to internal disorders. It was discerned, however, 'the literature' is substantially lacking in important background information on soil characteristics (e.g., texture, pH, and nutrient holding capacity), growing conditions (temperature, humidity, and rainfall), and other orchard characteristics that include fertilisation and irrigation management practices, biennial cropping effect, and insight into how these interacting factors mediate fruit quality and disorder susceptibility. To address this, future studies might seek to gather and report comprehensive data on edaphic and environmental characteristics and post-harvest conditions. Such more comprehensive data sets relating to fruit quality would contribute towards better understanding of implications for mango fruit quality, including IDs.

CRediT authorship contribution statement

Muhammad Asad Ullah: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Adhitya Marendra Kiloes:** Writing – original draft, Visualization, Methodology, Investigation. **Ammar Abdul Aziz:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Daryl Clifford Joyce:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

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