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Litchi Fruit Cracking: Insights into Physiological, Nutritional and Anatomical Traits

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ABSTRACT

Fruit cracking is a physiological disorder that severely affects litchi production and fruit quality, which ultimately causes economic loss to the growers. Despite its significant impact, it has not been previously investigated in detail. The present study was conducted with an aim to analyse cell wall-degrading enzymes, pericarp nutrient content and anatomical modifications associated with pericarp and pedicel of both healthy and cracked litchi fruits using light microscopy, stereomicroscopy and SEM (Scanning electron microscopy). The study revealed that peroxidase, cellulase and pectin methyl esterase activities were significantly higher in cracked fruits compared to healthy fruits in 'Dehradun' and 'Calcuttia' cultivars. Pericarp of cracked fruits had elevated N, P and Fe content in both litchi cultivars. However, K, Mg, Ca, Zn, Cu, B and Mn contents were substantially more in healthy fruits. The ultrastructure of pericarp in healthy and cracked litchi fruits shows significant differences in epidermal thickness and the appearance of microcracks, which have been confirmed with SEM and stereomicroscopic studies. Transverse sections of the stalk of both healthy and cracked litchi fruits depict distinct anatomical differences in the arrangement of vascular tissues. Xylem vessels of the pedicel of cracked fruits further reveal disintegration and reduction in the continuity of the vascular system that reduces translocation of solutes and solvent to the developing fruits.

Introduction

Litchi (*Litchi chinensis* Sonn.) is an important subtropical fruit which belongs to the family Sapindaceae. India is the 2nd largest litchi producer in the world after China, wherein it is cultivated on 1.02 lakh ha area with annual production of 6.0 lakh MT. It is commercially cultivated in the Indo-Gangetic plains and subtropical regions of West Bengal, Himachal Pradesh, Assam, Bihar, Haryana, Uttarakhand, Punjab, etc., due to the availability of suitable soil and climatic parameters. In Punjab province, the area under cultivation is 4,668 ha, with a production of 77,704 MT[1]. It is acknowledged as a highly valued crop due to its superb flavour, fragrance and sweetness. It is a rich source of antioxidants and offers several health benefits, including enhanced immune response, prevention of obesity, regulation of blood sugar levels and reduced risk of heart disease and cancer. However, litchi production is severely affected by physiological disorders such as fruit cracking and sunburning, which show significant effects on fruit quality and yield-related parameters and consequently reduce its market value. Cracking in fruit crops is triggered by disparities in climate, inheritance characteristics, nutrition, soil texture, structure, water potential, etc. Fruit cracking usually occurs when the internal pressure generated by fruit growth exceeds the capacity of pericarp to expand, which eventually causes the fruit to split. Fruit cracking generally occurs after the colour break stage and coincides with the onset of rapid aril expansion[2]. Cracking is mostly prominent during the final fruit growth development stage, where the actively growing aril exerts mechanical pressure on the relatively slow-growing or inactive pericarp that leads to fruit rupturing[3]. It is known to range from minor, superficial fissures that are confined to pericarp of the fruit to severe rupturing that extend along a substantial portion of the fruit length[4]. Both internal and external environmental factors contribute significantly to fruit cracking; however, Ca intake, higher temperature and reduced relative humidity are the main contributing factors. Higher

cracking incidence is reported when the temperature is > 38°C and RH is < 60 per cent, which results in about 10-25% crop losses[5]. Under higher humidity, the fruit's pericarp remains moist, allowing it to expand easily in response to the growing aril, which helps in preventing fruit cracking. In contrast, higher temperature leads to moisture losses in pericarp, making the fruit more prone to cracking[6]. Hot, dry and desiccating winds during the ripening process enhance the proportion of fruit cracking. Late-maturing cultivars are rarely affected due to the onset of the monsoon and sufficient moisture availability in the soil profile. In addition to varietal differences, significant temperature fluctuations between day and night, along with sudden and heavy irrigation after dry periods, also contribute substantially to the intensity of fruit cracking. This malady is further influenced by various factors, including anatomical, physical, nutritional, hormonal and soil moisture conditions[7]. It was reported that 'Dehradun' and 'Muzaffarpur' cultivars are prone to fruit cracking and nearly 33 per cent of fruits are lost[8]. Cracked fruits deteriorate quickly, making them susceptible to diseases and insect-pests. As a result, litchi has a short postharvest shelf life and becomes unmarketable, leading to significant economic losses to the growers[2].

The mechanical elasticity of the fruit peel and the rate of fruit growth play important roles in determining the occurrence of fruit splitting. Occurrence of cracking in fruit crops is also associated with physiological and structural changes within the fruit, including alterations in nutrient status, enzymatic activity and anatomical aspects of pericarp. The activities of cell wall degrading enzymes, including cellulase, pectin methyl esterase (PME), as well as wall-bound peroxidase (POD), were observed to be markedly higher in pericarp of the cracking-susceptible 'Nuomici' cultivar[9]. In contrast, the cracking-resistant cultivar 'Huaizhi' was characterised by higher content of structural Ca and galacturonans along with reduced activities of PME and ionically wall-bound POD[10]. These biochemical attributes help in the integration of phenolic cross-linking among cell wall polymers, thereby maintaining pericarp rigidity, extensibility and reducing susceptibility to fruit cracking. Nutrient status of soil, leaf and fruit tissues also plays a crucial role in influencing the intensity of fruit cracking. Several studies have shown that mineral balance in orchard soils, particularly exchangeable Ca content and organic matter, along with soil and pericarp N/K ratio is significantly associated with cracking susceptibility[11]. Litchi cultivars exhibit marked anatomical variation in peel structure that influences their susceptibility to fruit cracking. Cultivars characterised by well-organised mesocarp cells, compact spongy tissues in the lower mesocarp, reduced intercellular spaces and clearly defined endocarp boundaries show greater peel flexibility[12]. Peel cracking features are therefore considered reliable indicators of cultivar sensitivity. In the cracking-susceptible 'Nuomici' cultivar, surface fissures are wider and superficial than those observed in the resistant 'Huaizhi' litchi cultivar. Furthermore, cracked fruit pericarp displays smaller and pointed tubercles, reflecting restricted peel development, whereas non-cracked fruit peel exhibits tightly arranged and well-integrated crack junctions[11,2]. Rab and Haq (2012)[13] also reported that both fruit peel and pulp are closely associated with cracking susceptibility in litchi. Although several studies have examined the factors associated with litchi fruit cracking, physiological and structural modifications associated with this disorder are inadequately understood. Therefore, the present study was undertaken to compare healthy and cracked litchi fruits for pericarp anatomical alterations, enzymatic activity involved in cell wall modifications and nutritional composition of pericarp to study detailed mechanisms underlying fruit cracking.

Material and Methods

Plant material

The present investigation was conducted during 2025-26 at Department of Fruit Science, Punjab Agricultural University, Ludhiana and MS Randhawa Fruit Research Station, Gangian (Dasuya), Hoshiarpur (Punjab) on 49 years old, uniform and healthy litchi cultivars 'Dehradun' and 'Calcuttia'. All selected trees were maintained under uniform cultural practices throughout the entire study period. Healthy and cracked fruits of uniform size were harvested at physiological maturity and transported to the laboratory under a properly maintained cold chain. Fruits were thoroughly washed with ionised water for recording the observations. Ultrastructural features of both pericarp and pedicel were investigated using light microscopy, stereo microscopy and scanning electron microscopy (SEM) and detailed observations were documented.

Fruit cracking (%)

The fruit cracking percentage for each cultivar was determined using observations recorded from the outer canopy of respective plants and was calculated using the standard formula as

$$\text{Fruit cracking (\%)} = \frac{\text{Number of cracked fruits per panicle at time of harvest}}{\text{Number of fruits retained per panicle at the time of harvest}} \times 100$$

Enzyme activity for Peroxidase enzyme

Extraction

It was determined by following the method described by Thomas et al (1982)[14]. A 1 g sample of pericarp from healthy and cracked fruits was weighed and homogenised in a pre-chilled mortar and pestle using 10 mL of ice-cold potassium phosphate buffer (pH 7.5) containing 1% polyvinylpyrrolidone (PVP), 1 mM EDTA and 10 mM β-mercaptoethanol. The homogenate was then transferred into chilled centrifuge tubes and centrifuged at 11,000 rpm for 20 min. at 2°C. After centrifugation, any floating debris was removed by filtering the supernatant through cotton wool. The clear extract obtained was used for enzyme activity analysis.

Estimation

Peroxidase activity was assayed using guaiacol as the substrate. The reaction mixture consisted of 3 mL guaiacol solution, 0.1 mL hydrogen peroxide (H_2O_2) and 0.2 mL enzyme extract. The increase in absorbance was recorded at 470 nm for 3 min at 30 secs intervals, using deionised water as the blank. Peroxidase activity was expressed as the change in absorbance min^{-1} g^{-1} of fresh weight of fruit pericarp. The activity of peroxidase was calculated using the following formula:

$$\text{Enzyme activity} = \frac{\Delta A/\text{min} \times \text{volume made (ml)}}{\text{Volume of enzyme used} \times \text{fresh weight (g)}}$$

Cellulase enzyme

Extraction

The activity of cellulase was determined following the method described by Ali et al (2004)[15]. 10 g of fruit peel from healthy and cracked fruits were homogenised separately using a pre-chilled pestle and mortar. The homogenate was mixed with 20 mL of sodium citrate buffer (pH 4.6) containing 1 M NaCl, 13 mM EDTA, 1% polyvinylpyrrolidone (PVP) and 10 mM β-mercaptoethanol. The mixture was further homogenised and filtered through Whatman filter paper. The filtrate was then centrifuged at 15,000 × g for 30 min at 4 °C, and the clear supernatant was collected and used as the crude enzyme extract for determining cellulase activity.

Estimation

For cellulase activity determination, the reaction mixture consisted of 0.1 M sodium acetate buffer (pH 5.2), 1 ml of 0.5% CMC solution and 1 ml of enzyme extract. The mixture was incubated at 55°C for 1 hour. After incubation, 1 ml of DNS reagent was added to terminate the reaction. A blank was prepared by adding DNS reagent to the reaction mixture before incubation. The tubes were then boiled for 10 minutes to allow colour development and subsequently cooled to room temperature. Absorbance was recorded at 560 nm using a spectrophotometer. Enzyme activity was expressed as µg D-glucose released per gram of fresh weight per minute.

Pectin methyl esterase enzyme

Extraction

A 0.2 g sample of litchi pericarp was homogenised in citrate phosphate buffer (pH 5.0). The homogenate was centrifuged at 10,000 rpm for 15 minutes at 4°C. The resulting supernatant was collected and preserved at 4°C for further analysis.

Estimation

For the enzyme assay, 2 ml of 1% pectin solution was mixed with 2 ml of citrate phosphate buffer. Subsequently, 1 ml of the enzyme extract was added to the mixture. The reaction mixture was incubated at 35°C for 1 hour. Aliquots of 1 ml were withdrawn at 0 hours and after 1 hour of incubation and each sample was titrated against 0.005 N NaOH using phenolphthalein as an indicator. Enzyme activity was expressed as milliequivalents of esters hydrolysed per minute.

Nutritional content of peel

Nitrogen content (N) in the peel of healthy and cracked litchi fruits was estimated using the Kjeldahl method[16]. For estimation, 500 mg of dried and powdered peel sample from each treatment was used for digestion in a Kelplus Nitrogen Estimation System (Pelican Equipment, Chennai, India). Phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and micronutrients including iron (Fe), manganese (Mn), zinc (Zn), copper (Cu), and boron (B) were estimated following acid digestion of the samples. The samples were digested using a triple-acid mixture of nitric acid (HNO_3), perchloric acid

($HClO_4$), and sulfuric acid (H_2SO_4). Phosphorus content was determined using the vanado-molybdophosphoric yellow colour method[17], while potassium was estimated using a flame photometer[18]. Calcium, magnesium, iron, manganese, zinc and copper were quantified using an atomic absorption spectrophotometer (A Analyst 200, PerkinElmer, USA). Boron content was estimated using the azomethine-H method[19].

Anatomical characteristics

Light microscopy

For anatomical studies, fresh samples of healthy and cracked fruits from the litchi cultivars Dehradun and Calcuttia were collected. Hand sections of the fruit pericarp and pedicel were prepared by embedding the tissues in potato pith to facilitate smooth sectioning. The prepared sections were stained using the safranin-fast green technique[20] following the procedure outlined below. Initially, the sections were immersed in 2% aqueous safranin solution for 5 minutes. After staining, the sections were rinsed with water and passed through a graded alcohol series. Counterstaining was carried out by dipping the sections briefly in 2% fast green, followed by dehydration through alcohol, a 1:1 mixture of alcohol and xylene and finally pure xylene. The stained sections were then permanently mounted in DPX under a cover slip. Microscopic observations were made using a microscope fitted with a digital camera and computer-based imaging system equipped with NIS Elements F 3.0 software. The sections were examined at magnifications of 4X and 10X. Measurements of tissues from the fruit pericarp and pedicel were recorded at different points within each cross-section.

Scanning electron microscopy (SEM) and Stereomicroscopy

For Scanning Electron Microscopy (SEM) analysis, pericarp samples from both healthy and cracked fruits were cut into small pieces measuring approximately 0.5-1 cm^2. The samples were fixed overnight at 4°C in 2.5% (v/v) glutaraldehyde solution. After fixation, the samples were drained and washed three times with 0.1 M cacodylate buffer at 15-minute intervals. The buffer was then removed and the tissues were post-fixed in 1% osmium tetroxide for 1-2 hours at 4°C. Following osmium treatment, the samples were again washed three times with 0.1 M cacodylate buffer. Dehydration was carried out using a graded ethanol series (30%, 50%, 70%, 80%, 90% and 100% v/v). The dehydrated samples were subjected to critical point drying and subsequently kept in a vacuum desiccator overnight to ensure complete drying. The dried specimens were sputter-coated with a thin layer of gold to improve surface conductivity and then examined under a Scanning Electron Microscope available at the EMN Laboratory, PAU. The pericarp of healthy and cracked litchi fruits was also observed under a stereomicroscope to examine the surface morphology and detect the presence of microcracks.

SEM Examination

The samples were examined using a scanning electron microscope at the Central Instrumentation Laboratory, Central University of Punjab, Bathinda. SEM analysis was conducted to examine the pericarp surface morphology and ultrastructural characteristics, with particular emphasis on the differences between healthy and cracked fruits.

Statistical analysis

The experiment was carried out in 2025-26 using a randomised complete block design (RCBD). The differences between healthy and split fruits were analysed using an independent-samples t-test in Kaugrapes statistical software. Differences between the means were considered statistically significant at the 5% probability level ($p \leq 0.05$).

Results

Fruit cracking (%)

The results revealed (Table 1) that fruit cracking incidence differed significantly among the fruits located in different canopy directions in both litchi cultivars. In the 'Dehradun' cultivar, fruit cracking incidence was significantly higher in the south direction (T_2) (22.97%), followed by the west (T_4) (17.48%) and east (T_3) (12.59%) directions. However, fruits harvested from north of the canopy (T_1) recorded the lowest incidence of fruit cracking (8.57%). Similar observations were observed in the Calcuttia cultivar, wherein fruits from the southern canopy (T_2) recorded the maximum cracking of 8.56% and the minimum was recorded in North (T_1) (1.33%).

Table 1: Fruit cracking (%) in the outer canopy of Litchi cultivars

	Cracking (%)	
Treatments (Directions)	**Dehradun**	**Calcuttia**
T_1 (North)	8.57[a]	1.33[a]
T_2(South)	22.97[d]	8.56[d]
T_3 (East)	12.59[b]	3.33[b]
T_4(West)	17.48[c]	5.68[c]
CD (5%)	0.81	0.26

Enzymatic activity

Peroxidase activity

The peroxidase activity in pericarp of healthy and cracked fruits of 'Dehradun' and 'Calcuttia' cultivars was significantly higher (40.44 and 35.37 ΔA/min/g FW) in cracked fruits than in healthy fruits (37.45 and 32.23 ΔA/min/g FW, respectively) (Figure 1A and 2B).

Cellulase activity

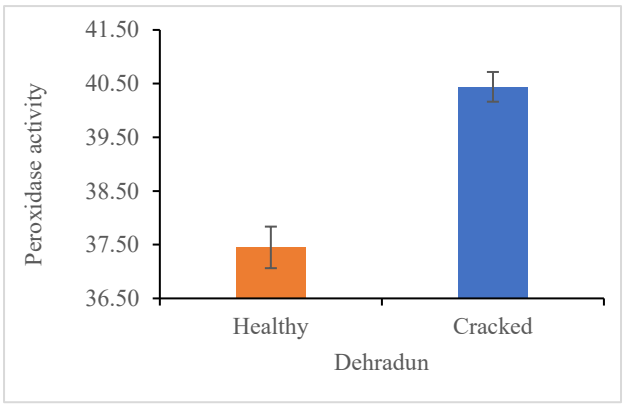
The results obtained for pericarp cellulase activity of healthy and cracked fruits of litchi cultivars revealed that pericarp cellulase activity of cracked fruits was observed to be substantially higher (18.04 µg glucose released/min/g FW) compared to healthy fruits (16.48 µg glucose released/min/g FW) in the 'Dehradun' cultivar. Similarly, higher cellulase activity of 16.71 µg glucose released/min/g FW was noted in cracked fruits of 'Calcuttia' in comparison to healthy fruits (15.45 µg glucose released/min/g FW) (Figure 1C and 2D).

Pectin methyl esterase activity

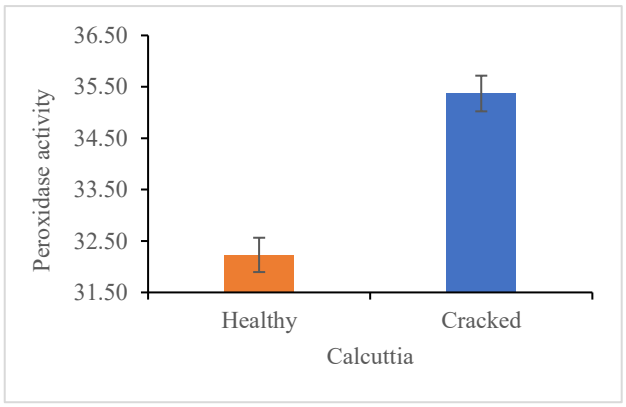
Pericarp of cracked fruits of 'Dehradun' cultivar had substantially higher (0.261 milliequivalent of esters hydrolysed/min) activity of pectin methyl esterase than healthy fruits (0.193 milliequivalent of esters hydrolysed/min). Likewise, 'Calcuttia' cultivar had higher PME activity of 0.247 milliequivalent of esters hydrolysed/min in pericarp of cracked fruits and it was lower in healthy fruits to the tune of 0.185 milliequivalents of esters hydrolysed/min (1E and 2F).

Fruit peel nutritional content

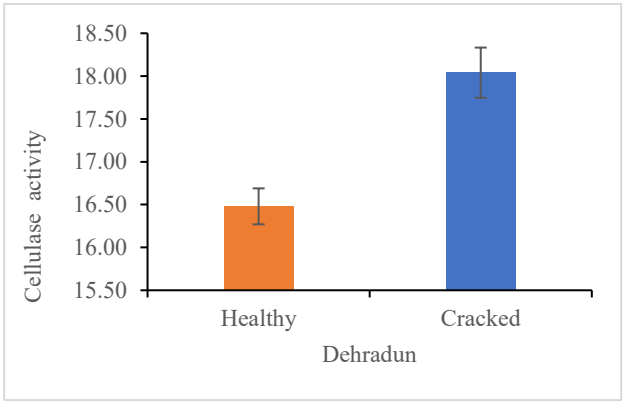
The nutritional composition of the peel differed significantly between healthy and cracked litchi fruits of both cultivars (Tables 2 and 3). Pericarp N (0.775 and 0.770%), P (0.115 and 0.112%) and Fe (80.64 and 74.31 ppm) content was considerably higher in cracked fruits than healthy fruits of 'Dehradun' and 'Calcuttia' cultivars, respectively. On the contrary, peel of healthy fruits had substantially higher contents of K (0.71 and 0.79%), Mg (0.271 and 0.178%), Ca (1.09 and 1.13%), Zn (29.41 and 26.74 ppm), Cu (11.28 and 13.08 ppm), Mn (23.05 and 19.12 ppm) and B (19.71 and 16.15 ppm) than cracked fruits of 'Dehradun' and 'Calcuttia' cultivars, respectively.



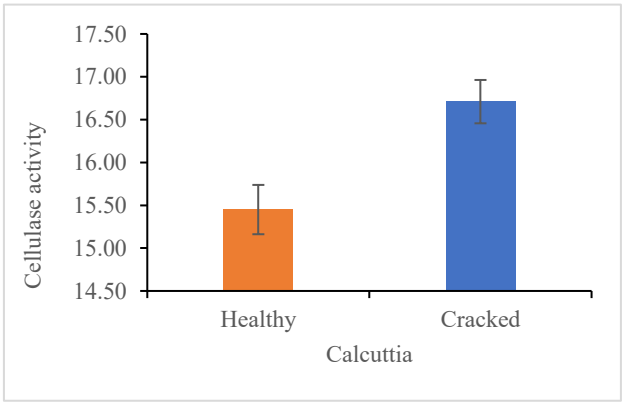
(A)



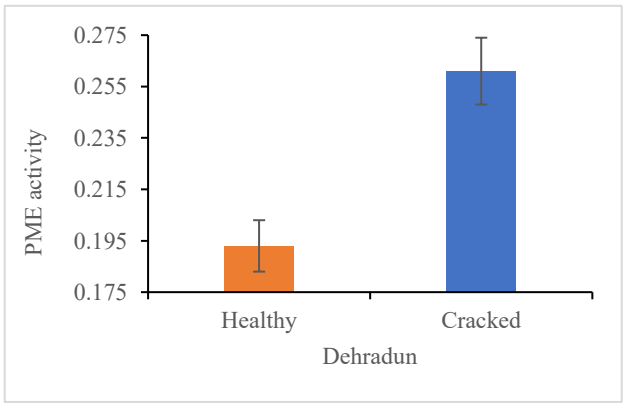
(B)



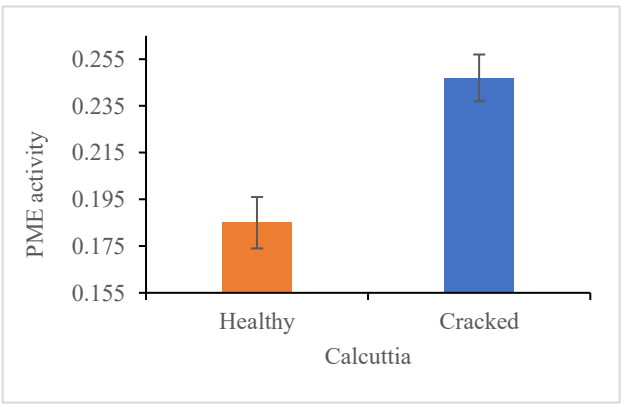
(C)



(D)



(E)



(F)

Figure 1: Comparison between the enzymatic activity of healthy and cracked fruits of Litchi cultivars: (A) Peroxidase activity in 'Dehradun' (B) Peroxidase activity in 'Calcuttia' (C) Cellulase activity in 'Dehradun' (D) Cellulase activity in 'Calcuttia' (E) PME activity in 'Dehradun' (F) PME activity in 'Calcuttia'

Table 2: Nutrient content in peel of Litchi *cv.* Dehradun

Treatment	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	Fe (ppm)	Zn (ppm)	Cu (ppm)	Mn (ppm)	B (ppm)
Healthy	0.742 ± 0.011	0.084 ± 0.006	0.71 ± 0.026	1.09 ± 0.035	0.271 ± 0.008	61.12 ± 1.343	29.41 ± 0.849	11.28 ± 0.350	23.05 ± 0.411	19.71 ± 0.412
Cracked	0.775 ± 0.009	0.115 ± 0.008	0.56 ± 0.024	0.82 ± 0.025	0.248 ± 0.007	80.64 ± 1.712	20.32 ± 0.711	9.21 ± 0.232	19.67 ± 0.394	17.18 ± 0.358
t (P ≤ 0.05)	S	S	S	S	S	S	S	S	S	S

Table 3: Nutrient content in peel of Litchi *cv.* Calcuttia

Treatment	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	Fe (ppm)	Zn (ppm)	Cu (ppm)	Mn (ppm)	B (ppm)
Healthy	0.745 ± 0.005	0.095 ± 0.005	0.79 ± 0.025	1.13 ± 0.036	0.178 ± 0.006	57.51 ± 1.233	26.74 ± 0.765	13.08 ± 0.368	19.12 ± 0.367	16.15 ± 0.370
Cracked	0.770 ± 0.004	0.112 ± 0.003	0.62 ± 0.021	0.84 ± 0.028	0.154 ± 0.007	74.31 ± 1.458	19.22 ± 0.718	10.61 ± 0.247	16.31 ± 0.260	13.76 ± 0.307
t (P ≤ 0.05)	S	S	S	S	S	S	S	S	S	S

Anatomical characteristics

Light microscopy

Cross section of pericarp

The transverse section of healthy and cracked litchi pericarp depicts distinct anatomical differences (Figure 1). The healthy pericarp possessed a continuous, compact and relatively thick epidermal layer, forming an intact protective barrier over the fruit surface. In contrast, cracked pericarp exhibited a disrupted epidermis characterised by the presence of microcracks. The epidermal thickness was higher in healthy fruits (67.65 μm) compared to cracked fruits (41.99 μm). These observations suggested that weakening of the epidermal layer and the formation of microcracks are associated with the initiation of fruit cracking in litchi.

Cross section of pedicel

Microscopic examination of transverse sections of pedicels from healthy and cracked litchi fruits revealed marked differences in the arrangement and structural organisation of the vascular tissues (Figure 2). In the healthy pedicel, vascular bundles were well developed, compact and uniformly arranged in a circular pattern. The xylem and phloem tissues were clearly differentiated and properly aligned, indicating an intact vascular system capable of efficiently transporting water, minerals and photosynthates. In contrast, the pedicel of cracked fruits exhibited noticeable alterations in vascular organisation. The vascular bundles appeared comparatively less compact and irregularly arranged, with disruption of their normal radial orientation. In some patches, adjacent vascular bundles appeared partially fused or distorted and xylem tissues showed disorganisation with reduced continuity of the vascular system. The area of xylem vessels (Table 4) was significantly higher (313.34 μm^2) in the pedicel of healthy fruits than in cracked fruits (230.97 μm^2), which had distorted xylem vessels.

Stereomicroscopy and scanning electron microscopy

Stereomicroscopic and scanning electron microscopy (SEM) studies of litchi peel surface suggest significant structural differences between healthy and cracked fruits (Figures 3 and 4). The peel surface of healthy fruits exhibited a compact, continuous and intact epidermal layer with closely arranged polygonal tubercles and no visible surface disruptions. In contrast, peel surface of cracked fruits showed the presence of numerous microcracks (mc) distributed along the epidermal ridges and between adjacent tubercles. Under stereo microscopy, these microcracks appeared as fine fissures and discontinuities on peel surface, while SEM analysis provided detailed information. Epidermal cells of cracked fruits appear disorganised and fragmented, with evident separation and rupture of the cuticular layer. The occurrence of microcracks indicates loss of peel integrity and mechanical strength, which may act as initiation sites for the development of macrocracks leading to fruit cracking. These observations confirmed that microcrack formation is closely associated with the cracking susceptibility of litchi fruits.

Discussion

Fruit cracking (%)

Fruit development in litchi follows a biphasic growth pattern that plays a central role in the mechanism of fruit cracking. The first growth phase (Stage I) is characterised by the gradual growth of pericarp and seed coat, while the second phase (Stage II) involves rapid enlargement of the aril and embryo, which begins once the pericarp has almost attained maximum size[8,9]. During the final stage of fruit growth, the actively expanding aril exerts substantial internal pressure on pericarp, which at this stage exhibits limited growth, thereby increasing the incidence of fruit cracking[3]. Huang and Xu (1983)[21] proposed the "ball skin-bladder" theory wherein the relationship between the pre-grown pericarp and the expanding aril during the second phase of fruit development is noted. Accordingly, fruit cracking occurs when the coordinated growth of the pericarp (ball skin) and aril (bladder) is disrupted. With aril expansion, the resulting internal pressure may exceed the tensile strength of pericarp, exerting an increasing strain on the peel that eventually makes the fruit prone to cracking[11]. Cracking susceptibility varies significantly among litchi cultivars, indicating that genetic background plays an important role in determining their resistance or susceptibility to fruit cracking. In addition, the position of fruits within different canopy directions results in varying exposure to sunlight, which consequently influences their susceptibility to cracking. Kumar et al. (2001)[22] reported a higher incidence of litchi fruit cracking on the south and west sides of the tree canopy, which was attributed to higher temperatures, greater light intensity and longer exposure to sunlight. In contrast, fruits on the north and east directions remained relatively shaded, except during the early hours. Light conditions

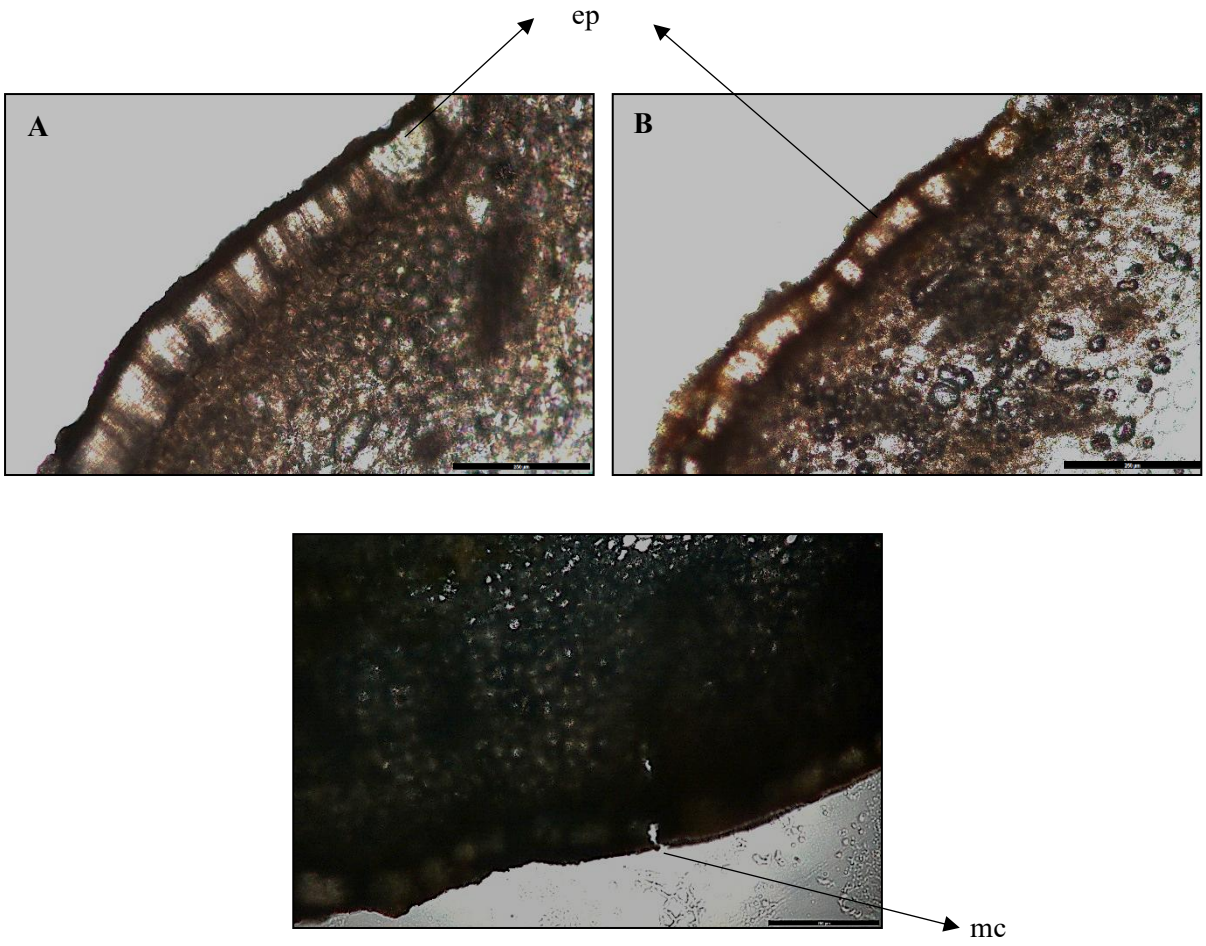


Fig 1: Cross section of pericarp of litchi fruit
A. TS of healthy peel
B. TS of cracked peel
(ep: epidermis, mc: microcracks)

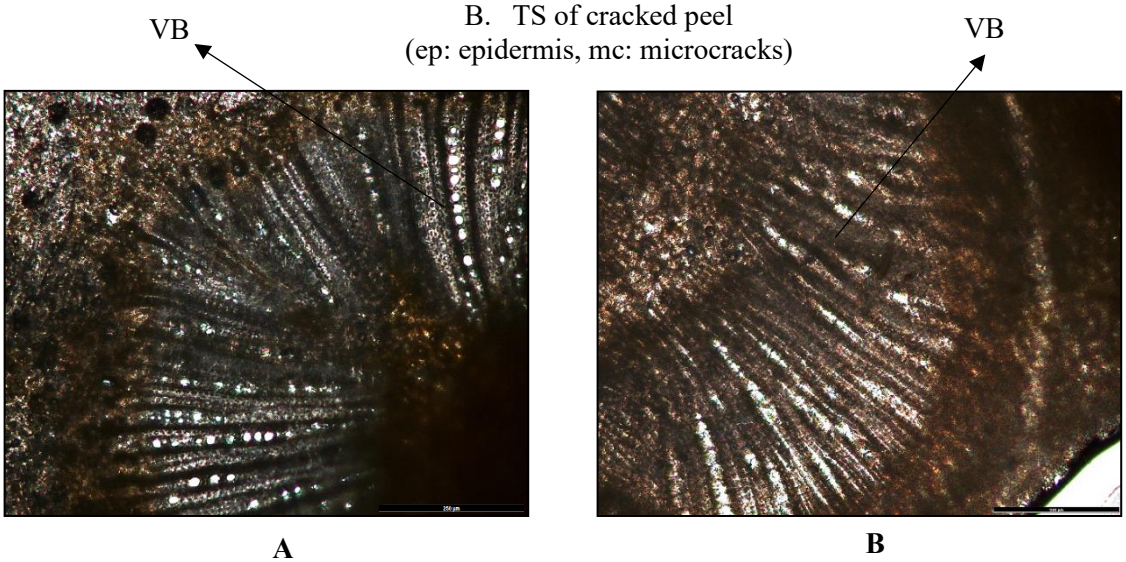


Fig 2: Cross-section of pedicel of litchi fruit

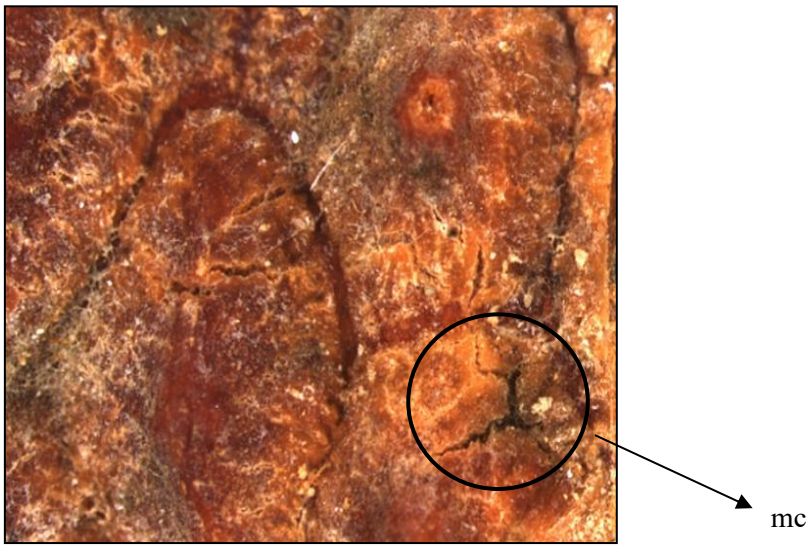
A: TS of healthy fruit; B: TS of cracked fruit
(VB: Vascular bundle)

Table 4: Epidermal thickness of pericarp of healthy and cracked Litchi fruit

Treatments	Epidermal thickness (µm)	Pericarp thickness (mm)	Area of xylem vessels (μm^2)
Healthy	67.65 ± 4.497	0.77 ± 0.013	313.34 ± 16.07
Cracked	41.99 ± 2.443	0.71 ± 0.019	230.97 ± 10.26 (disrupted)
t ($P \leq 0.05$)	S	S	S



A



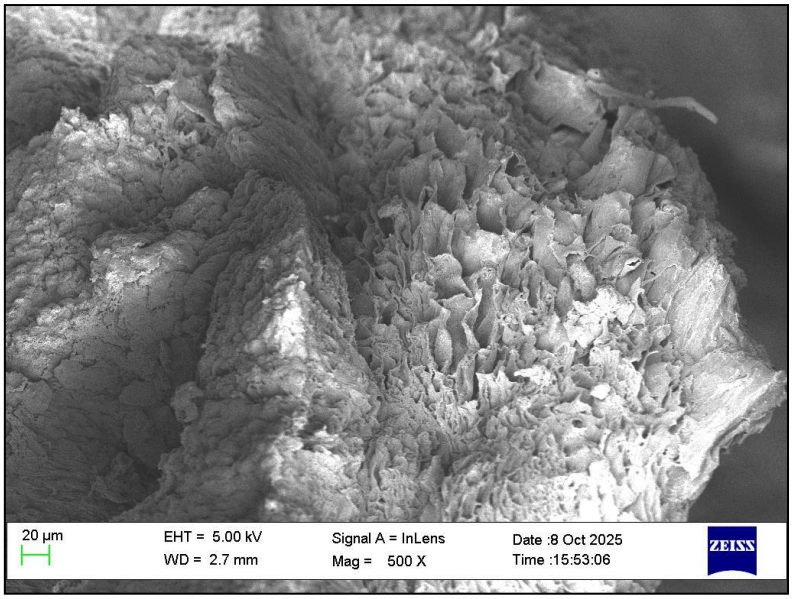
B

Fig 3: Stereomicrographs of peel

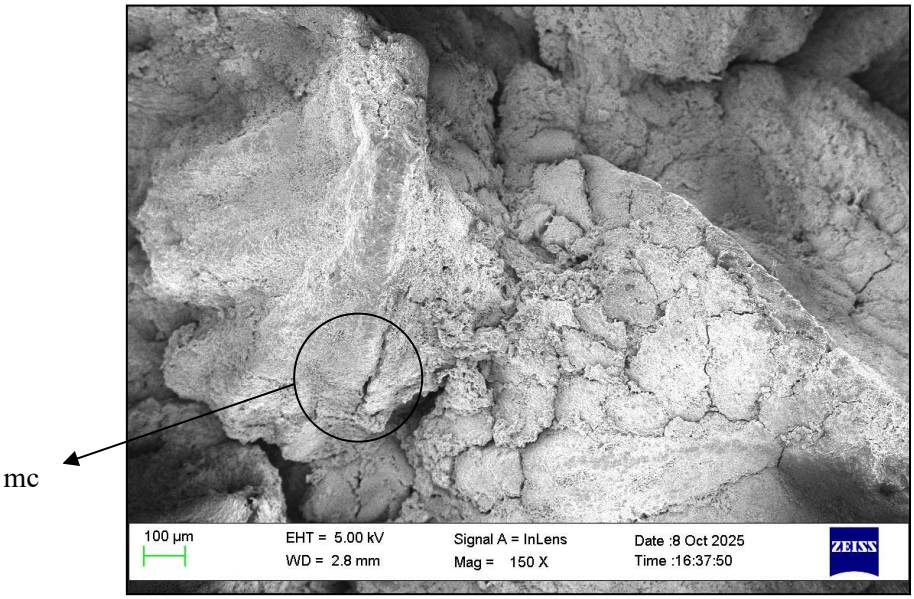
A: Healthy peel surface

B: Cracked peel surface

mc=microcracks



A



B

Fig 4: Scanning electron microscopy of pericarp of litchi fruit

A: Healthy peel surface

B: Cracked peel surface

(mc=microcracks)

such as intensity, quality and angle of light intercepted by the plant likely influence gene expression, plant metabolism and fruit growth and thereby make fruits susceptible to physiological disorders[23].

Enzymatic activity

It is observed that pericarp of cracked fruits exhibits significantly higher cellulase activity, peroxidase activity and pectin methyl esterase (PME) activity than healthy fruits in both 'Dehradun' and 'Calcuttia' cultivars. The activity of cell wall-modifying enzymes, including PME and PG (polygalacturonase), helps to regulate pectin metabolism and promote fruit softening during the early stages of fruit development[24]. It was reported that peel of 'Nuomici' cultivar was susceptible to cracking and possessed higher activity of cell-wall degrading enzymes such as PG, PME, PPO (polyphenol oxidase), cellulase and POD[9]. Whereas, crack-resistant 'Huaizhi' cultivar showed higher structural Ca and galacturonan content and lower wall-bound POD and PME activity[10]. These traits help maintain phenolic cross-links between cell wall polymers and regulate the integrity and extensibility of pericarp, thereby lowering the fruit's susceptibility to cracking.

Peroxidase activity assists in oxidative degradation of phenolic compounds, leading to the formation of brown polymers[25]. Cell wall hydrolases and oxidoreductase enzymes are correlated with cracking in citrus[26]. These enzymes facilitate the degradation of cellular polysaccharides, resulting in weakening of fruit peel. Campa (1991)[27] reported that oxidoreductases, particularly peroxidase, facilitate the formation of phenolic cross-links among structural proteins, hemicelluloses and pectin, while also promoting lignification. These modifications reduce cell wall elasticity and increase its rigidity. Such alterations to the mechanical properties of fruit peel during development have been linked to cracking in *Citrus* species. Likewise, Kaur et al. (2022)[26] in lemon and Liu et al. (2022)[28] in pepper also recorded higher peroxidase activity in cracked fruits.

The abscission process is accompanied by a pronounced increase in cellulase activity. These enzymes are known to participate in the degradation of the adhesive cell wall components that bind the cells of the abscission zone together and the increase in their activity reduces the fruit break strength[29]. Cellulase has also been considered an important enzyme that regulates fruit softening by degrading the cellulose in fruit cell walls[30].

Nutritional content of pericarp

The results indicated that peel of cracked fruits contained higher levels of N, P and Fe than healthy fruits in both litchi cultivars. However, the content of K, Mg, Ca, Zn, Mn, Cu and B was found substantially higher in the peel of healthy fruits than cracked fruits. The results suggested that higher levels of N, P and Fe in fruit pericarp might encourage fruit cracking. Similar findings were reported by Hepaksoy et al. (1998)[31] and Hasan and Chattopadhyay (1996)[32]. Likewise, Sharma and Ray (1987)[33] and Sharma and Dhillon (1987)[34] observed that cracked fruits had higher N and P content but lower Ca and Zn content than normal fruits.

It is evident from the results that both macronutrients (K, Ca, Mg) and micronutrients (Zn, Mn, Cu, B) are essential in reducing the incidence of fruit cracking in litchi cultivars. Calcium and potassium are integral components of the cell wall and are essential for cell wall development, cell enlargement and the maintenance of osmotic balance and cellular turgor potential. Insufficient availability of these nutrients can impair peel integrity and increase the incidence of physiological disorders, including peel breakdown and fruit cracking in citrus crop. Cronje et al. (2011)[35] suggested that mineral imbalance, particularly Ca deficiency, contributes to rind breakdown in 'Nules Clementine'. Similarly, Alva et al. (2006)[36] reported that fruits with lower K concentrations developed thinner peel, making them more susceptible to cracking. Likewise, Morgan et al. (2005)[37] demonstrated that increased K levels enhanced rind thickness in 'Hamlin' oranges and proposed that thicker rinds may reduce the incidence of fruit cracking in susceptible cultivars.

Boron plays a fundamental role in maintaining cell wall structure by participating in the synthesis of pectic substances, improving cell membrane elasticity and preventing the disintegration of vegetative tissues. It also facilitates sugar translocation and contributes to the formation of structural components of the cell wall. Boron deficiency reduces the amount of calcium bound to pectic compounds, highlighting its involvement in Ca metabolism within the cell wall[38]. Significant differences in boron concentration between healthy and cracked fruit peels were also documented by Wang and Qin (1987)[39]. Huang et al. (2004)[40] demonstrated that higher Ca concentration together with thicker cuticle and spongy tissue layers are main characteristics associated with resistance to fruit

cracking. Several studies have confirmed that cracked fruits have lower concentrations of essential mineral nutrients than healthy fruits. Kaur et al. (2022)[26] reported significantly higher concentrations of Ca, K and B in peel of non-cracked lemons than cracked fruits. Comparable observations were reported in oranges by Sallato et al. (2017)[41] and Hardiyanto et al. (2022)[42]. Likewise, Josan et al. (1995)[43] observed reduced calcium and boron concentrations in peel of cracked 'Baramasi' lemon fruits compared with healthy fruits.

Magnesium is known to activate certain enzymes included in physiological processes like photosynthesis, respiration and synthesis of DNA and RNA. Its deficiency leads to premature defoliation, decreased development of roots and production of smaller fruits with thin peels, which results in a higher incidence of fruit cracking[44]. Zinc is involved in regulating the activity of various enzymes that are involved in carbohydrate metabolism and photosynthesis and helps improve water absorption[45]. It also reduces the formation of the abscission layer and promotes cell wall strengthening. Copper plays an essential role in chloroplast formation by regulating the production of carbohydrates, proteins and nitrate reduction processes. It also protects chlorophyll from untimely damage, which affects the photosynthesis and enzyme formation processes[46].

Anatomical characteristics

Light microscopy

Light microscopy is used to examine transverse sections of fruit pericarp and pedicel. The study revealed distinct anatomical differences between healthy and cracked litchi fruits, indicating that alterations in the structural organisation are associated with fruit cracking. The pericarp of healthy fruits possessed continuous, compact and intact epidermal layers, whereas cracked fruits exhibited disruption of the epidermis along with the presence of microcracks. Since the epidermis serves as the primary protective barrier against mechanical injury and water losses, the formation of microcracks represents the initial stage of peel failure, which might subsequently develop into visible cracks under increasing internal pressure during fruit growth. Similar microcracking of the litchi pericarp has previously been reported during fruit development in association with aril expansion[47]. The presence of these microcracks may indicate localized weakening of the pericarp and could make the fruit susceptible to extensive fruit cracking[48].

The organisation and integrity of the peel are the most important factors determining its susceptibility to fruit splitting. Peel thickness and hardness are main indicators of peel strength and can directly affect the occurrence of splitting. Thicker peel is generally better able to withstand stretching and deformation, making the fruit less prone to cracking[26]. Cultivars with thicker peels have been reported to show a lower incidence of splitting than those with thinner peel. Splitting develops through several distinct stages[49]. Initially, the peel appears normal, but as the fruit approaches the critical stage, visible symptoms such as a brown stripe, cuticular fractures and cracks begin to appear. During later stages, peel becomes thinner as the pulp continues to expand, increasing the tension exerted on the peel. This increasing tension can eventually cause tissue breakdown and the formation of microcracks on the outer surface, which may subsequently develop into visible fruit cracking[26]. The initial symptoms of microcracking in the rind develop in the epicarp and mesocarp, possibly due to rapid pulp development during fruit growth[50]. Changes in the mechanical properties of the peel, together with disorganisation of the subepidermal cells, have also been associated with fruit splitting[51]. In damaged tissues, the cytoplasm becomes disorganised, which may impair cellular osmoregulation and cause the loss of cellular lipids. Similar differences have been reported in tomato, where cracking-resistant fruits possess more compactly arranged subepidermal cells than cracking-susceptible fruits[52]. Thus, the shape, density and arrangement of subepidermal cells may also contribute to differences in susceptibility to fruit splitting.

As a terminal organ, the fruit receives most of its nutrients from plant through the connecting pedicel, which transports them via the xylem/ apoplastic pathway, the phloem/ symplastic pathway or through both pathways. Fruit growth usually depends on the supply of assimilates, water and mineral ions transported through pedicel[53]. Therefore, pedicel plays an important role in fruit development and yield. The pedicel of healthy litchi fruits exhibits well-developed and uniformly arranged vascular bundles with clearly differentiated xylem and phloem tissues. In contrast, pedicels of cracked fruits show irregularly arranged and comparatively less compact vascular bundles, with distortion and partial fusion of adjacent bundles. Such structural weakening has been associated with environmental stresses, nutrient imbalance, and other physiological stresses[54]. Fruit splitting may begin in the inner peel along

the regions associated with vascular bundles. Deformation of the vascular tissues, together with reduced epidermal thickness, can weaken the peel and make it more vulnerable to rupture. Uneven or rapid water uptake through the vascular system has been suggested as a factor contributing to this process[55]. This is particularly important when a period of water deficit is followed by a sudden increase in water availability. The resulting rapid influx of water can cause cells within the fruit to expand quickly, increasing internal pressure and eventually leading to epidermal rupture. Rapid fruit growth may also involve uneven cell division and expansion, further contributing to epidermal weakness and changes in the structure of the vascular bundles. Hence, the structure and function of the vascular tissues are important for explaining translocation of water, minerals and assimilates from the pedicel into the fruit and their distribution within peel. Studies on small citrus plants bearing fruits have shown that a substantial proportion of water movement occurs through the xylem, which forms an important part of the transpiration stream. Fruit growth has also been reported to be influenced by the rigidity of the pericarp cell walls[56]. Likewise, water entering the fruit through the phloem may contribute to an increase in internal fruit pressure. Adequate water supply through the xylem can help maintain plant water status and reduce the effects of water stress, which might influence the susceptibility of fruits to cracking[57]. These structural changes might impair the continuity of vascular transport and influence the movement of water and assimilates into the developing fruit.

Stereomicroscopy and scanning electron microscopy

SEM studies and stereomicroscopy confirmed that fruit cracking is associated with disruption of the continuity and integrity of the pericarp surface. The SEM images provide morphological evidence that microcracks are present in cracked fruits, whereas the healthy fruit maintains a comparatively continuous surface. Microscopic cracks are small cracks confined to the cuticle that do not extend into the epidermal or hypodermal cell layers. They develop as a result of stress and strain imposed on the fruit surface and are typically oriented perpendicular to the direction of the major strain. Their formation is promoted by surface wetness and high humidity[58]. Although cracks may initially remain restricted to the cuticle, they compromise its barrier function, allowing greater water uptake into the fruit as well as increased water loss through transpiration[59]. It has been suggested that microcracks can progressively develop into larger and visible macro-cracks[60]. Grimm et al. (2019)[61] also reported that structural defects such as microcracks can act as initiation sites for fruit cracking by locally impairing the barrier function of the cuticle. External forces can not only enlarge pre-existing microcracks but also create new sites of stress concentration, thereby increasing the severity of fruit cracking[62]. A ruptured, disorganised and rougher peel texture in cracked fruits, compared with the smooth and uniform peel observed in healthy fruits, was also reported by Kaur et al. (2024)[55] in 'Daisy' mandarin.

Conclusion

The study revealed that fruit cracking in litchi is associated with differential sunlight exposure and temperature, enhanced activity of cell wall-modifying enzymes, nutritional imbalance and structural weakening of the pericarp. Cracking was highest on the south-facing canopy in both 'Dehradun' and 'Calcuttia'. Cracked fruits showed higher peroxidase, cellulase and PME activities, along with lower Ca, K, Mg and several micronutrients. Anatomical and SEM observations further confirmed epidermal disruption, microcrack formation and altered vascular organisation in cracked fruits. Overall, fruit cracking seems to be related to the combined effect of environmental, biochemical, nutritional and anatomical factors**.**

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Declarations

Data availability

The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Compliance with guidelines and legislation

The experimental research and collection of plant material were conducted in accordance with the relevant institutional, national, and international guidelines and legislation.