



Article

The Link between Mineral Elements Variation and Internal Flesh Breakdown of 'Keitt' Mango in a Steep Slope Mountain Area, Southwest China

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Abstract: Internal flesh breakdown (IFB), a serious physiological disorder of mango fruit, causes significant economic losses in Southwest China. We investigated the extent of IFB in 100 mango orchards and how changes in the mineral nutrients of fruit flesh, leaves and soil affect IFB. We found that 76% of the mango orchards showed IFB symptoms, and the average IFB incidence was 10%. Fruit flesh with IFB showed higher average contents of N, P, K and Mg, lower average Ca content and higher average ratios of N/Ca, K/Ca and Mg/Ca. The leaves from orchards with IFB symptoms exhibited a remarkable increase in the average N and Mg contents. No significant difference was observed in the soil nutrient concentrations between orchards with and without IFB fruit. IFB incidence was significantly positively correlated with the N/Ca, K/Ca and Mg/Ca ratios in the fruit flesh. However, when considering individual orchards with IFB symptoms, fruit flesh that exhibited breakdown symptoms had Ca content higher, lower than or equal to that of the healthy fruit flesh. There was a strong correlation between fruit flesh and leaf in the same mineral elements, but neither of them showed a significant correlation with soil. Considering the mango trees were cultivated on steep slopes, and fertilizer was applied at a fixed position, we hypothesized that long-term fertilization in the partial root zone led to the excess of N, K and Mg in soil, which reduced the total flesh Ca content or resulted in the abnormal cellular distribution of Ca in the flesh, and ultimately triggered IFB development.

Keywords: mango; disorder; Ca deficiency; partial root-zone fertilization



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1. Introduction

Mango fruit, which is a popular subtropical and tropical fruit known for its sweet, unique aroma and abundant carotenoid content, has recently become the fifth most important fruit crop, with an annual production of approximately 52 million tons [1]. However, internal flesh breakdown (IFB), which is considered a physiological disorder in mangoes, often occurs during pre-harvest ripening and post-harvest storage [2,3]. The IFB symptom starts as spongy and water-soaked tissue at the flesh closer to the seed and eventually becomes brown–black and spreads to the whole fruit flesh tissues. The disorder affects internal fruit quality and results in fruit unfit for human consumption. The IFB has been found in many mango varieties in global mango-growing regions [2–5] and is a serious problem for the mango industry.

Although a few studies have addressed this problem, the causes and mechanisms involved in IFB development are not well understood. The predisposition to developing IFB has been linked to genetic factors, unsuitable application of synthetic fertilizers, high temperatures and sudden changes in humidity [2,5,6]. The level of fruit development and ripening conditions also affect the susceptibility of mango to IFB, and there is a dramatic increase in their tendency to develop IFB at the later stages of fruit development [5,6]. Mango trees grown in acidic soils have a higher risk of IFB than those grown in alkaline soils [7]. Subraman et al. [8] observed that IFB incidence in mango fruit increased from high relative to low humidity. Many researchers have attributed IFB development to the deficiency of one or more mineral nutrients, particularly calcium (Ca), deficiency in fruit [2,3,5,6]. However, increasing Ca input through foliar and/or fruit application is not always an effective measure to prevent IFB in mangoes [5,6]. It was reported that bagging mango fruit with polyethylene covers reduced the tendency of IFB, possibly since bagging increased fruit transpiration rate to that increased with Ca content moving into fruit [6]. Muhammad et al. [5] found that pre-harvest foliar application of 4% calcium chloride (CaCl_2) solution reduced the incidence of IFB in mango ('Samar Bahisht Chaunsa'), but post-harvest fruit treatment with 1% CaCl_2 did not yield notable effects. Moreover, several studies have shown that IFB is not the result of Ca deficiency [4,9,10]. Therefore, thorough studies are needed on how and why fruit Ca nutrition affects the mango fruit.

China is the second-largest mango producer in the world after India, with a cultivation area of 2.27 million hectares and a production of 18 million tons in the 2017 growing season [11]. In Southwest China, the dry-hot valleys of the Jinsha River (a branch of the Yangtze River) are the largest producers, with a cultivated area of 70,667 ha and a production of 570,000 tons year⁻¹ [12]. Fruit grown in the dry-hot valleys of the Jinsha River have good appearance and sensory quality and a low incidence of pests and diseases because of adequate solar and hot resources, low air relative humidity and large temperature differences between day and night. In addition to the special climate conditions, notably in the area, mango orchards have been established on land with slopes varying from 15° to 50°, with almost no flat land (Figure 1). Although the steep-slope planting pattern of mango trees has led to more economical and ecological profitability, growers need to spend considerable amounts of human resources and investment for irrigation, fertilizer and pest management. 'Keitt' mango is the leading commercial cultivar in the region and occupies 90% of the total cultivated land because of late maturation, high disease resistance and high yield. However, this cultivar is susceptible to IFB (Figure 2). The frequent occurrence of IFB has become a bottleneck for mangoes in the studied area.

To promote the development of the mango industry and provide valuable information for improving mango fruit quality and optimizing mango cultivation management, this study aimed (1) to investigate the extent of IFB in 'Keitt' mango grown on the steep slopes of mountains in Southwest China; (2) analyze the relationship between IFB occurrence and changes in mineral nutrient concentrations in the fruit flesh, leaf and soil; and (3) discuss the leading mineral factors for causing IFB development.

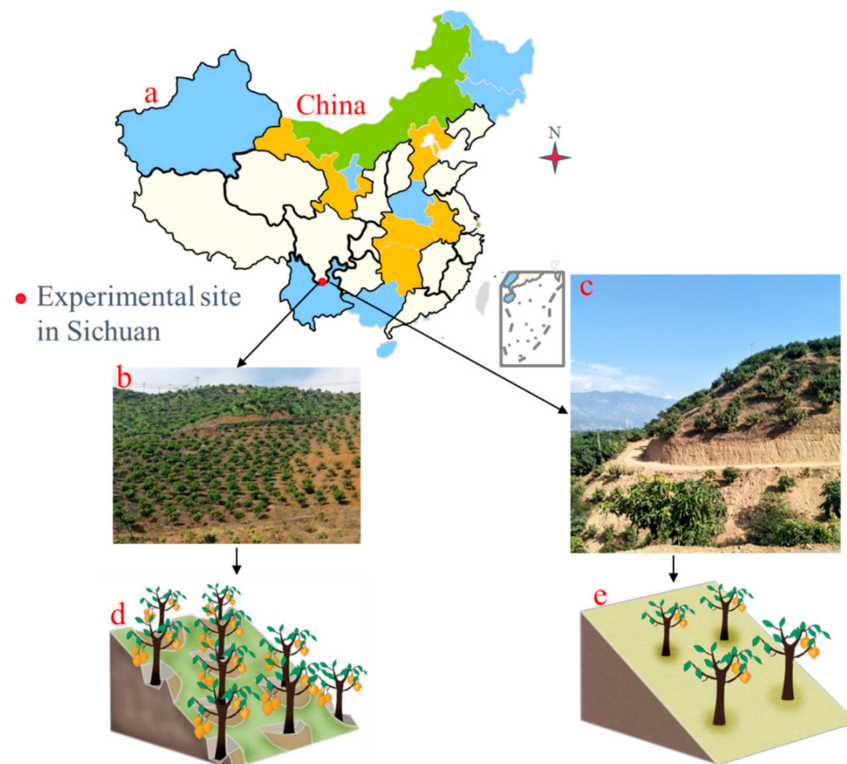


Figure 1. Location of the study sites in China (a) in the Jinsha River of Southwest China. Photo of a mango tree on fish-scale pits (b) and natural slopes (c). Schematic diagram of a mango tree on fish-scale pits (d) and natural slopes (e).



Figure 2. Phenotypical IFB symptoms in mango 'Keitt' fruit.

2. Materials and Methods

2.1. Study Area Description

The experimental sites were located in the dry-hot valley of the Jinsha River in Panzhihua City ($101^{\circ}08' - 102^{\circ}15' E$, $26^{\circ}06' - 27^{\circ}21' N$), Sichuan Province, Southwest China. The elevations of the region ranged from 937 to 4195.5 m above sea level. The region benefits from a subtropical monsoon climate with distinct dry and rainy seasons. The average annual air temperature is $20.3^{\circ}C$. Average annual rainfall ranges from 900 to 1300 mm and is concentrated between June and November, the annual evaporation is

2750.9 mm and the average relative humidity (RH) is 55%. The mean monthly temperature and RH during the experimental period in 2020 are shown in Figure 3. Mango orchards are established in a typical mountain area with altitudes varying from 937 to 1700 m and steep slopes varying between 15° and 50° (Figure 1). The region typically has no frost all the year. According to the United States Department of Agriculture (USDA) soil classification system (http://www.nrcs.usda.gov/Internet/FSE_DOCUMENTS/nrcs142p2_051232.pdf, accessed on 5 June 2021), the soil of the study area is a reddish-brown loam soil with a pH of 7.0, organic matter of 11.0 g kg⁻¹, alkali-hydrolyzable nitrogen of 35.0 mg kg⁻¹, available phosphorus of 8.0 g kg⁻¹ and available potassium of 152 mg kg⁻¹ at 0–20 cm depth. These data are from China's second national soil survey [National Soil Survey Office (NSSO)] in the early 1980s.

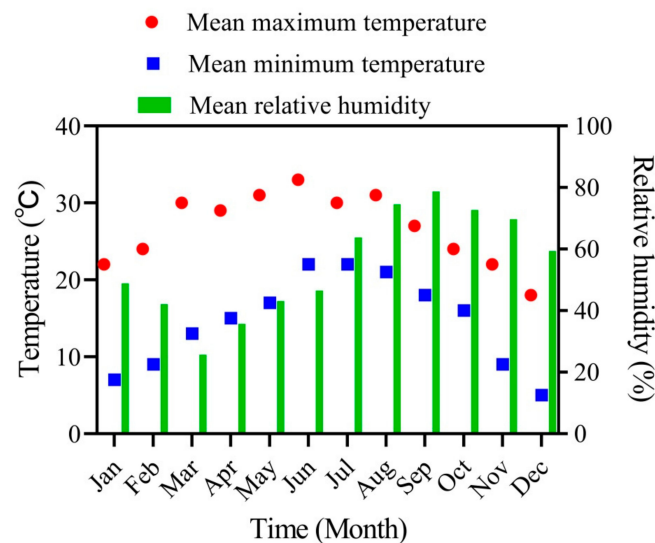


Figure 3. Mean monthly temperature and relative humidity during the experiment in 2020.

2.2. Fruit, Leaf and Soil Sampling

One hundred representative commercial mango orchards of cv. 'Keitt' (12 to 16 years old) were randomly selected along the slope from 15° to 50°. The total area of each orchard is more than 1 ha, and the density of the mango trees ranges from 610 to 650 trees ha⁻¹. For each orchard, nine trees with even and similar loads were randomly selected in triplicate. The distance between the sample trees was at least 6 m. From each tree, 15 expanded healthy leaves from bearing, and non-bearing branches and 20 fruits were sampled 80 days after full bloom (the second fruit fast expansion stage) and 150 days after full bloom (fruit commercial maturity stage) from four directions (east, south, west and north) around the tree in the 2020 fruit season, respectively. A total of 135 leaves and 180 fruits were sampled from each orchard. For each orchard, all harvest mangoes were longitudinally cut into two parts to evaluate IFB according to the typical symptoms of IFB (Figure 2). The number of fruits showing typical IFB symptoms was counted. IFB incidence was calculated as follows:

$$\text{IFB incidence (\%)} = (\text{Number of fruit with IFB symptom} / \text{Total fruit number}) \times 100\%.$$

The flesh of the healthy and the disordered fruits was oven-dried at 70 °C and ground into fine powder. The leaves were washed gently in distilled water to remove dust on the leaf surface, dried with absorbent papers, oven-dried at 70 °C and ground into fine powder.

Soil samples were collected in June and July (after the fruit's first fast growth) in 2020. This was conducted to ensure that the sample points were uniform and representative. The soil sample points were roughly evenly distributed over the mango orchards. In each sampling orchard, six soil cores (5 cm in diameter) were collected from the 0 to 40 cm soil layer to avoid fertilization and bulked into one composite soil sample. After air-drying at room temperature, all visible plant residues and stones were handpicked from the

samples. Then, the soil samples were ground with a mortar and pestle and sieved through a 2 mm sieve.

2.3. Analytical Methods

The plant (fruit flesh and leaf) samples were digested with $\text{H}_2\text{SO}_4\text{--H}_2\text{O}_2$ to quantify the contents of nitrogen (N) by the Kjeldahl method using a Kjeldahl nitrogen apparatus (FOSS-2100, FOSS, Switzerland), phosphorus (P) by the molybdenum yellow method using a UV spectrophotometer (UV-2700, Shimadzu Scientific Instruments) and potassium (K) by the flame emission photometry method using a flame photometer (M410, Sherwood, England) [13]. The contents of calcium (Ca) and magnesium (Mg) in the plant samples were analyzed using an atomic absorption spectrophotometer (Analytikjena, AA-350, Analytik Jena AG, Jena, Germany) after microwave-assisted digestion with HClO_4 and HNO_3 (1:4, *v/v*) [13].

Soil pH was measured using a pH meter in a deionized soil and water suspension 1/5 (*w/v*), soil organic matter (OM) was determined by potassium dichromate titration, soil total nitrogen (TN) was determined by the Kjeldahl method, soil alkaline-hydrolyzed nitrogen (AN) was determined using an H_3BO_3 solution followed by steam distillation, soil available phosphorus (AP) was measured colorimetrically after $0.5 \text{ mol L}^{-1} \text{ NaHCO}_3$ extraction (1:10 *w/v*) and soil available potassium (AK) was analyzed using the flame emission photometric method after $1.0 \text{ mol L}^{-1} \text{ CH}_3\text{COONH}_4$ extraction [13]. Soil available Ca (ACa) and Mg (AMg) concentrations were analyzed using an atomic absorption spectrophotometer (Analytikjena, AA-350, Analytik Jena AG, Jena, Germany) after acid digestion in $\text{HNO}_3\text{--HClO}_4$ (*v/v* = 3/1) [14].

2.4. Statistical Analysis

Analysis of variance (ANOVA) was performed to detect the statistical difference using Duncan's multirange test at the significance levels of $p < 0.05$ (*) and $p < 0.01$ (**). Correlations between experimental variables were determined using Pearson's correlation coefficient, with the significance level set at $p < 0.05$. All statistical analyses were performed using Statistical Analysis System (SAS) (v 8.1, SAS Institute, Inc., Cary, NC, USA).

3. Results

3.1. IFB Incidence in Mango Orchards

The incidence of IFB in 100 mango orchards was evaluated. Of the 100 mango orchards, 76 showed IFB symptoms of variable degrees and magnitudes, and the average value of IFB incidence was 10%. The IFB incidence in 76 orchards ranged from 2.0% to 37.5%, with a mean value of 13%. Of these infected orchards, the IFB incidences in 11, 25, 15, 15 and 10 mango orchards were 1–5%, 5–10%, 10–15%, 15–20% and >20%, respectively (Figure 4).

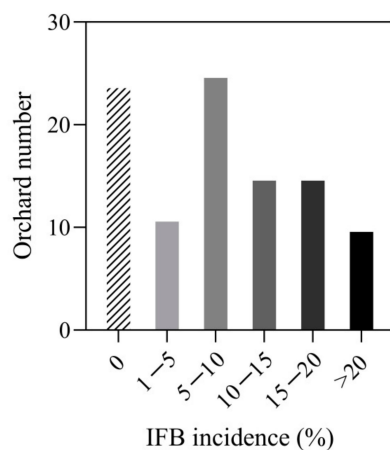


Figure 4. The distribution of IFB incidence evaluated in 100 mango orchards.

3.2. Variation of Mineral Element Concentrations between the Flesh of Healthy Fruit and Fruit with IFB

To investigate the mineral elements in fruit flesh associated with the development of IFB, we measured the N, P, K and Mg content in the flesh of healthy fruit and fruit with IFB in the 100 sampled orchards. The average values of flesh N, P, K and Mg contents in the fruit with IFB were significantly higher than those in the healthy fruit flesh (Figure 5). Pearson's correlation analysis showed no significant relationship between the N, P, K and Mg concentrations and IFB incidence. The average flesh Ca content was significantly lower in fruit with IFB than in healthy fruits. Moreover, the incidence of IFB was negatively and significantly correlated with fruit flesh Ca content ($r = -0.034$, $p = 0.000$) (Figure 6).

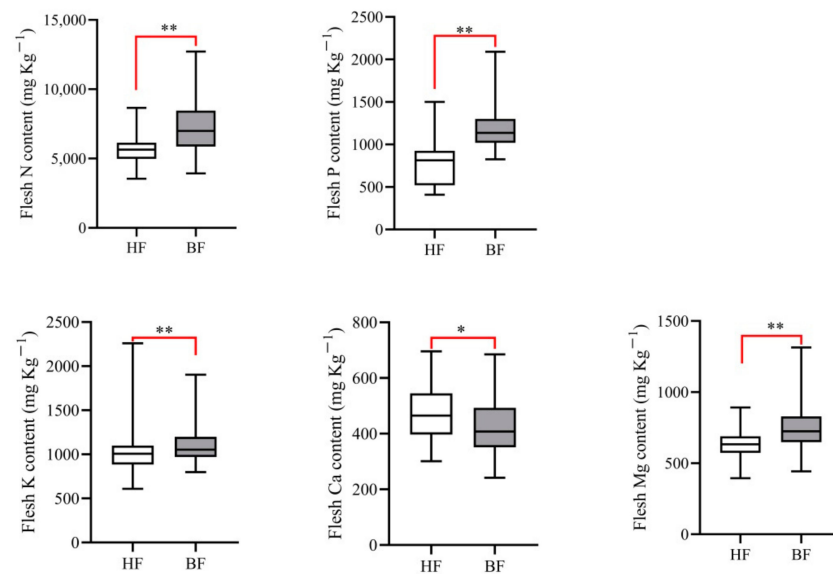


Figure 5. Box plots of N, P, K, Ca and Mg content in the healthy fruit flesh and internal flesh breakdown (IFB) fruit flesh. The highest and lowest quartiles are displayed above and below the box, and the line in each box represents the mean value. HF and BF represent the flesh of healthy fruit and fruit with IFB, respectively. Significant differences were determined by one-way ANOVA test: *, $p < 0.05$; **, $p < 0.01$; The same as below.

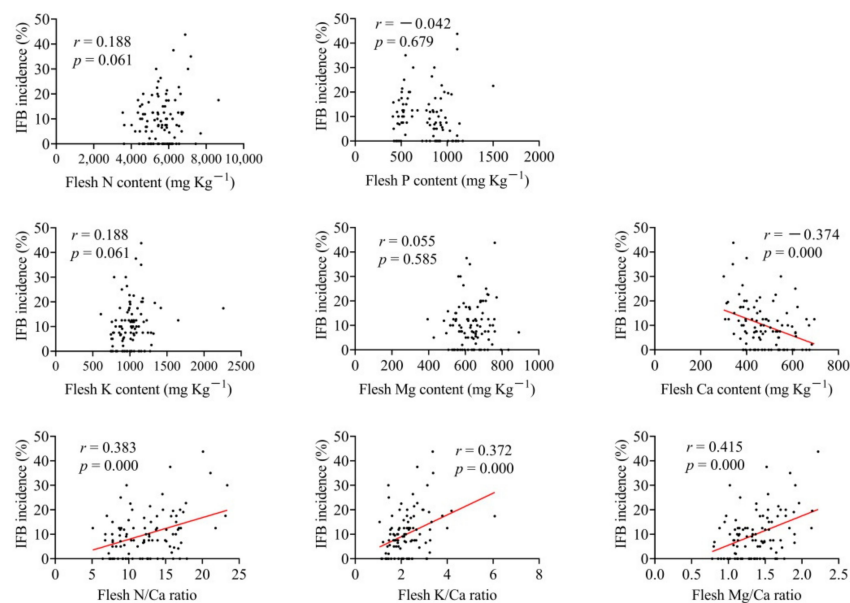


Figure 6. Relationship between IFB incidence and flesh N, P, K, Mg and Ca contents and flesh N/Ca, K/Ca and Mg/Ca ratios in 100 mango orchards.

To further elucidate the relationship between total flesh Ca concentration, and IFB development, the potential differences in Ca content between healthy and IFB fruits from 76 infected orchards were analyzed. The IFB fruit flesh displayed high Ca content in 19 orchards, low Ca content in 40 orchards and 17 orchards with similar Ca content compared to healthy fruit flesh within the same orchard (Figure 7). These results indicate that low Ca concentration is the important factor resulting in IFB, but the incidence of IFB is not always related to low total Ca content in mangoes.

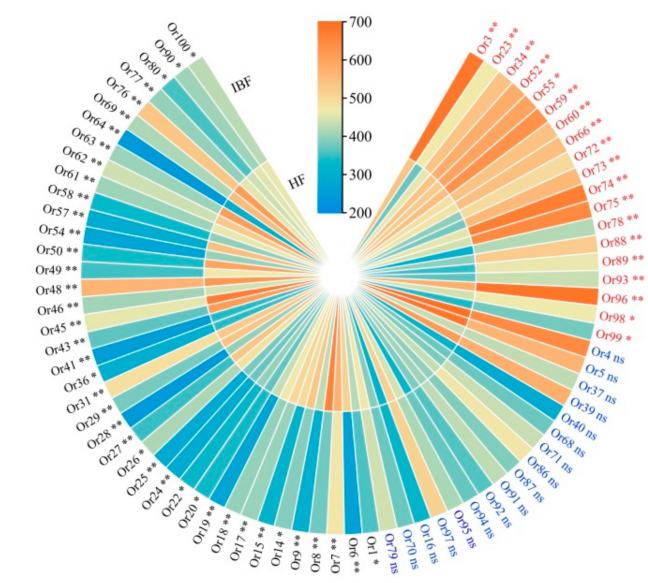


Figure 7. Heat map of Ca content (mg kg^{-1}) in the healthy fruit flesh (HF) and the internal flesh breakdown fruit flesh (IBF) in the same orchard (Or). Blue and orange indicate low Ca content and high Ca content. Significant differences were determined by one-way ANOVA test: *, $p < 0.05$; **, $p < 0.01$; ns, no significant difference.

To explore the effects of nutrient balance on IFB development, we compared the N/Ca, K/Ca and Mg/Ca ratios in healthy fruit flesh and IFB fruit flesh. The IFB fruit flesh had significantly higher average N/Ca, K/Ca and Mg/Ca ratios (Figure 8), suggesting that the Ca content was relatively lower than the N, K, and Mg contents. As shown in Figure 6, IFB incidence displayed significant ($p = 0.000$) positive correlations with the ratios of N/Ca, K/Ca and Mg/Ca in the flesh, where, $r = 0.383$, $r = 0.372$ and $r = 0.415$, respectively.

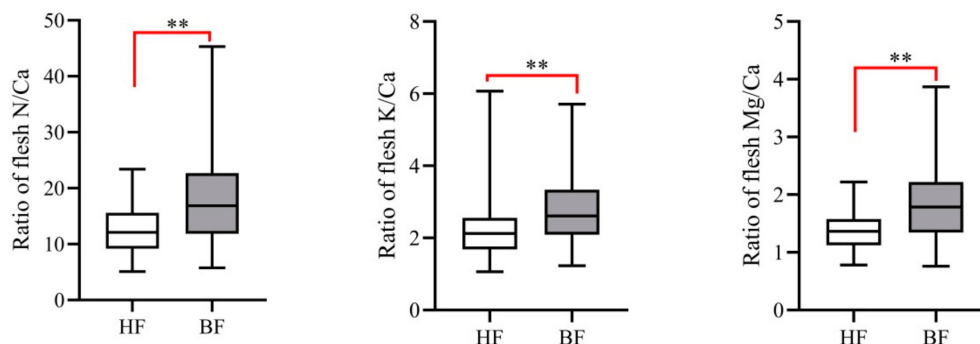


Figure 8. Box plots of flesh N/Ca, K/Ca and Mg/Ca ratio in the healthy fruit and the internal flesh breakdown fruit. HF and BF represent the flesh of healthy fruit and fruit with IFB, respectively. Significant differences were determined by one-way ANOVA test: **, $p < 0.01$.

3.3. Variation in Leaf Mineral Element Concentrations between Orchards with and without IFB Fruit

To examine the mineral elements in leaves involved in IFB development, we compared the differences in leaf N, P, K, Ca and Mg concentrations between samples from 76 orchards with IFB fruit and 24 healthy orchards without IFB fruit. As shown in Figure 9, the mean concentrations of leaf N and Mg in the affected orchards were significantly higher than those in healthy orchards. However, the mean concentrations of leaf P, K and Ca were similar in orchards with and without IFB fruit. Leaf N, P, K, Ca and Mg levels were not significantly correlated with the incidence of IFB (Figure 10).

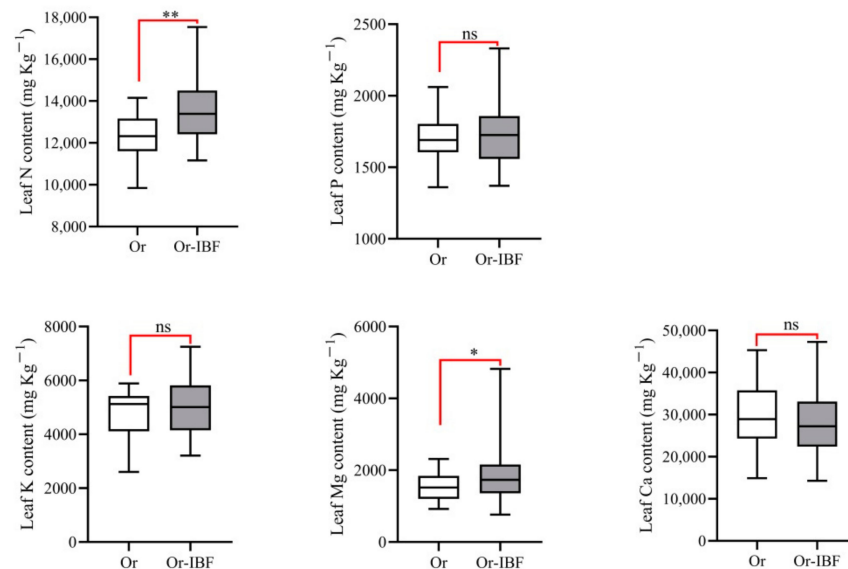


Figure 9. Box plots of leaf N, P, K, Mg and Ca content in the orchard without and with internal flesh breakdown (IFB) fruit. Or and Or-IBF represent 24 mango orchards without IFB fruit and 76 mango orchards with IFB fruit, respectively. Significant differences were determined by one-way ANOVA test: *, $p < 0.05$; **, $p < 0.01$; ns, no significant difference.

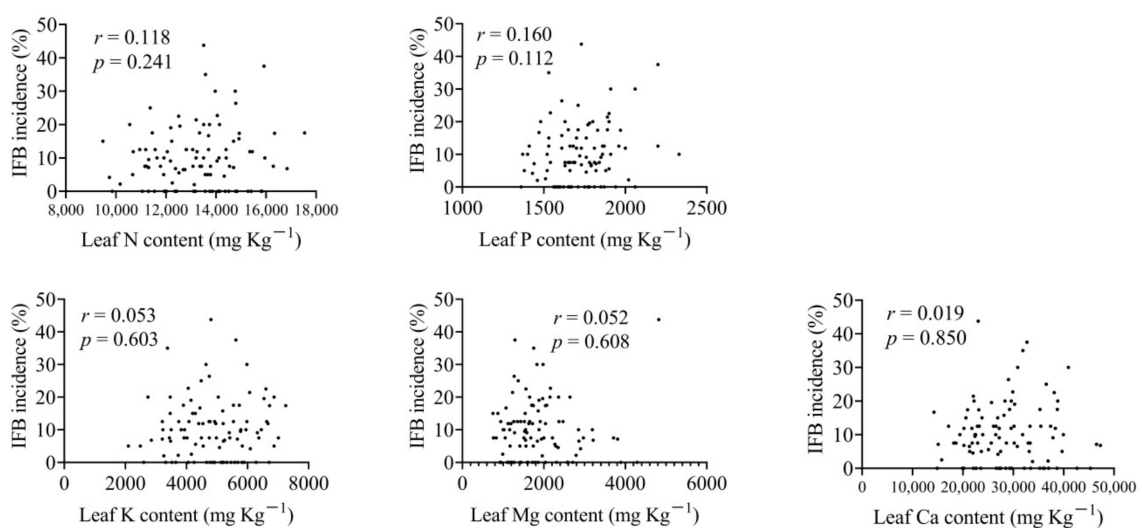


Figure 10. Relationship between IFB incidence and leaf N, P, K, Mg and Ca content in 100 mango orchards.

3.4. Variation of Soil pH and Nutrient Contents between Orchard with and without IFB Fruit

To explore the relationship between soil mineral nutrition status and IFB development, levels of soil pH, organic matter (OM), available nitrogen (AN), total nitrogen (TN), avail-

able phosphorus (AP), available potassium (AK), available calcium (ACa) and available magnesium (AMg) were measured in 100 mango orchards. As Figure 11 show, there were no significant differences in the average soil pH values, OM, AN, TN, AP, AK, ACa and AMg between orchards with and without IFB fruit. We also found no significant correlations between soil pH, OM, AN, TN, AP, AK, ACa and AMg and the incidence of IFB (Figure 12).

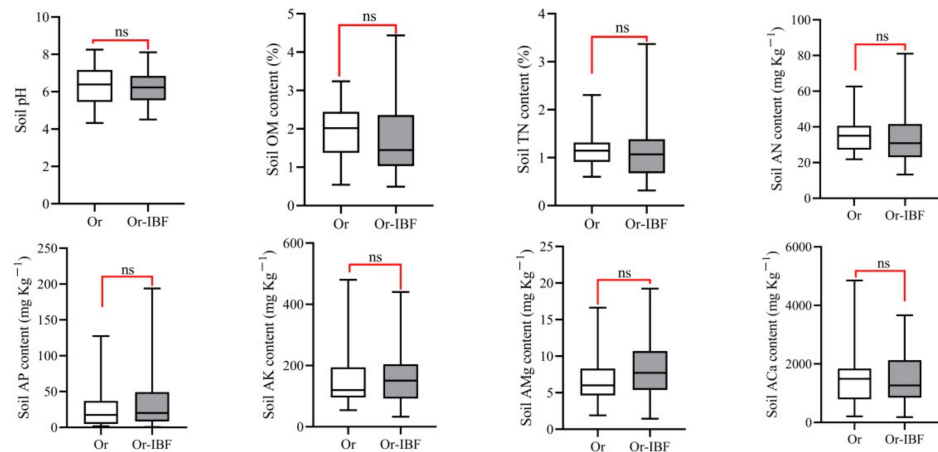


Figure 11. Box plots of soil pH and mineral nutrient contents in the orchard with and without IFB fruit. Or and Or-IBF represent 24 mango orchards without IFB fruit and 76 mango orchards with IFB fruit, respectively. OM: organic matter, TN: total N, AN: available N, AP: available P, AK: available K, AMg: available Mg, ACa: available Ca. Significant differences were determined by one-way ANOVA test: ns, no significant difference.

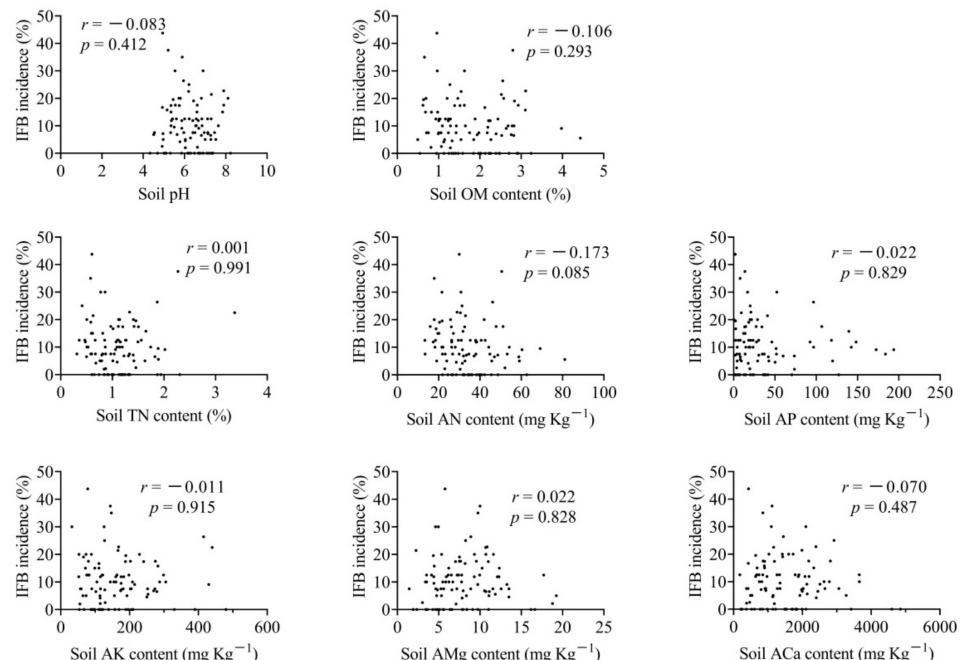


Figure 12. Relationship between internal flesh breakdown incidence and soil pH and mineral nutrient contents in 100 mango orchards. OM: organic matter, TN: total N, AN: available N, AP: available P, AK: available K, AMg: available Mg, ACa: available Ca.

3.5. Correlation Analysis of Nutrient Concentration in Fruit Flesh, Leaf and Soil

To study the soil–plant nutrient relationships, the strength of the correlations among all pairs of nutrient concentrations in fruit flesh, leaf, and soil were measured. As shown in

Figure 13, there were significant positive correlations between fruit flesh and leaf for the same mineral elements, such as flesh N and leaf N, flesh P and leaf P, flesh K and leaf K, flesh Ca and leaf Ca and flesh Mg and leaf Mg, with $r = 0.381$, $r = 0.344$, $r = 0.270$, $r = 0.334$ and $r = 0.504$, respectively. A negative correlation was also found between flesh Ca and leaf N or flesh N, with $r = -0.409$ and $r = -0.531$, respectively. Notably, there was no significant correlation between soil and fruit flesh or leaf for the same mineral element.

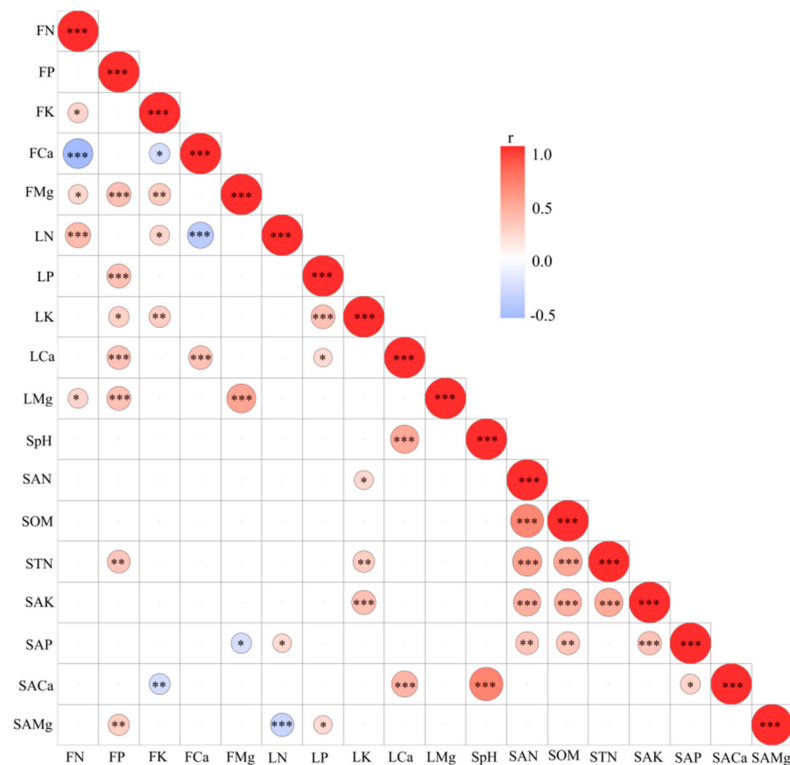


Figure 13. Spearman correlation heat map showing correlations among nutrient concentrations in fruit flesh, leaf and soil in 100 mango orchards. F: flesh, L: leaf, S: soil. Only significant values ($p < 0.05$) are shown. Red and blue colors represent significant positive correlations and negative correlations. Darker color represents stronger correlations. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

4. Discussion

Insufficient or excessive content of mineral nutrients in fruit tissues can induce developmental and metabolic disorders during fruit development and ripening [15–17]. For instance, the deficiency of zinc (Zn), boron (B) and K in the peel resulted in citrus fruit creasing [15], and low peel Ca content could cause the development of superficial scald in pear fruit [18]. High susceptibility of bitter pit in apples has been associated with high contents of N, K and Mg in fruit tissue [16]. In the present study, ‘Keitt’ mango showed a high occurrence of IFB since 76% of the orchards were affected. We found that the nutritional status of plants strongly affects the occurrence of IFB in mango fruits. The IFB fruit flesh had higher average N, P, K and Mg contents but lower average Ca content than healthy fruit flesh. IFB incidence was only negatively correlated with flesh Ca content, and no significant correlation was found between IFB incidence and flesh N, P, K or Mg content, suggesting that Ca deficiency may be a key factor involved in the occurrence of IFB. However, it is surprising that no difference in the average Ca content of the leaves between orchards with and without IFB fruit was observed in our study. Additionally, there were significant differences in IFB incidence among mango trees within the same orchard under the same soil [19]. Moreover, within the same tree, some mango fruit flesh breakdown was noted, while others there was not [20], suggesting that the fruit’s ability to acquire Ca was different among fruit individuals. These facts implied that IFB development in mango

fruits might not entirely be caused by soil Ca deficiency in mango orchards. This result is understandable because Ca accumulation in growing fruit is highly determined by the continuous provision of Ca absorbed by roots from the soil; the process of Ca delivery was affected by a great many factors such as temperature, irrigation, soil conditions and light; thus, fruit Ca deficiency may not entirely result from low Ca availability in the soil [21,22].

The development of fruit Ca deficiency symptoms is closely linked to the absorption, transport, allocation and utilization of Ca, except for the lack of soil Ca [23–26]. It is generally accepted that root-absorbed Ca is transported into fruit by transpiration, high N in the soil leads to increased plant N content, stimulating leaf growth and the transpiration rate, which are known to reduce Ca movement to the fruit [27]. On the other hand, high N levels lead to rapid fruit growth that dilutes the limited Ca content in fruit to some extent and drives the development of Ca deficiency symptoms [28,29]. Consistent with previous studies, our study showed that the average N content in both leaves and flesh was significantly increased in infected orchards. The fruit flesh Ca content was negatively correlated with leaf N content, and IFB incidence was also positively correlated with the N/Ca ratio. At the cellular level, K and Mg compete with Ca for membrane-binding sites but do not assume the role of Ca in membrane structure and function. This may compromise the integrity of the cell membranes and result in electrolyte leakage and consequently inducing cell death and tissue collapse [14,29]. In these cases, imbalances of nutrient supply resulted in ‘relative Ca deficiency’ in fruit. In the present study, higher K/Ca and Mg/Ca ratios were observed in the IFB fruit flesh than in healthy fruit flesh. In addition, we found that the K/Ca and Mg/Ca ratios in the flesh showed a strong positive correlation with IFB incidence. Similarly, in the pear fruit with the internal disorder [30] and the apple fruit with bitter pit [31], higher N/Ca, K/Ca and Mg/Ca ratios were also found compared to the healthy fruit. These results highlight that the nutritional balance of N-Ca, K-Ca and Mg-Ca in fruit tissues is vital during fruit development. Therefore, the mechanism underlying the imbalance between N, K or Mg and Ca should be given more attention when analyzing the impact of mineral nutrient factors on IFB development in mango fruit. Ensuring a balance of N-Ca, K-Ca and Mg-Ca is also a challenging task for developing effective cultivation techniques and resolving fruit Ca deficiency symptoms in the future.

Most studies indicated that fruits with Ca deficiency symptoms, such as blossom-end rot in tomato [32], bitter pit in apple [31] and hard end in pear [14], had similar or even higher total Ca content than healthy fruits. These results prompted us to further investigate the relationship between IFB development and the total flesh Ca content. After comprehensive comparison of the amount of Ca between IFB fruit and healthy fruit, we found that fruit flesh with IFB symptoms had high, low or similar Ca levels compared to the healthy fruit flesh. Therefore, IFB development in mango ‘Keitt’ fruit is not always a consequence of a reduction in the total flesh Ca content. Despite sufficient Ca content in the flesh, the “Ca deficiency disorder” may be due to abnormal cellular Ca partitioning and distribution. This would explain why calcium supplementation is not an effective control practice for IFB in the field. However, recent findings on tomatoes [33], apples [31] and pears [14] indicate that there is not a simple causal relationship between reduction of total tissue Ca content and development of Ca deficiency symptoms and that localized Ca deficiency within the cell could be the cause of the development of the Ca deficiency disorder. Further studies are required to determine whether the finding of IFB development in mango fruit with lower total Ca content is in line with previous observations.

Soil contains essential nutrients and water, which are the main sources of plant growth and development. The nutritional quality of field soils is essential for maintaining crop yield and quality [34]. The generally accepted idea is that analysis of soil nutrient status may indicate the capacity of soil to supply nutrients to the plant and is often used as a basis for recommending fertilization management [35,36]. Unexpectedly, no differences in soil pH and mineral nutrients between mango orchards with and without IFB fruit were found in this study. Meanwhile, the same mineral element contents in fruit flesh and leaf were

significantly correlated with each other, such as flesh N with leaf N, flesh K with leaf K and flesh Ca with leaf Ca. However, the same mineral element concentration in the soil was not significantly related to that in the fruit flesh or leaves. Thus, we hypothesize that soil nutrient availability does not reflect or influence nutrient availability in mango orchards in the dry-hot valleys of the Jinsha River. The lack of soil-plant nutrient relationships found here may be attributed to the steep slope planting pattern of mango trees in the region. The mango trees on steep slopes were fertilized at a fixed position adjacent to the trunk of the mango tree every year. We infer that it is possible that supplying nutrients fixed to one part of the root zone and leaving the other part a long time without fertilizer application results in uneven distribution of soil nutrients in mango orchards. In the present study, soil samples were collected away from the fertilization position to avoid sampling of the applied fertilizers. Therefore, our investigation of the nutrients in these samples revealed the properties of the original soil without fertilization application but did not reveal the effects of long-term fertilization application on soil nutrient availability in the root zone.

Together with our results and previous findings, we propose a model to delineate the cause of IFB development in mango fruit (Figure 14). The long-term fixed fertilization on the steep slopes may cause excessive nutrients in the partial root-zone soil, especially the accumulation of N, K and Mg. Unevenly distributed nutrients may promote uptake of nutrients by the roots from the nutrient-rich zone. As a result, leaf N and Mg contents are upregulated, further enhancing leaf transpiration rate and leaf Ca uptake and consequently reducing total fruit flesh Ca content due to slow Ca movement into the fruit, which ultimately leads to IFB development in mango fruit. In contrast, partial root-zone excessive fertilization increased the fruit flesh N, K and Mg contents without negatively or positively affecting fruit Ca acquisition; however, this resulted in abnormal cellular Ca partitioning and distribution, leading to a cellularly localized Ca deficiency in the fruit flesh, and ultimately triggering IFB development in mango fruit. To date, the effects of partial root drying on water use efficiency and plant growth have been extensively studied [37–39], but the effects of partial root fertilization on plant nutrition and growth have hardly received attention. To our knowledge, only one publication reported that patchy fertilizer application stimulated root nutrient uptake and improved the biomass yield of oilseed rape [40]. Future investigations about the relationship between partial root-zone fertilizer supply and IFB development in mango fruit are needed in pot and field experiments. Collectively, our findings might provide new insight for preventing the disorder of mango fruit grown on steep slopes in the mountainous area of Southwest China.

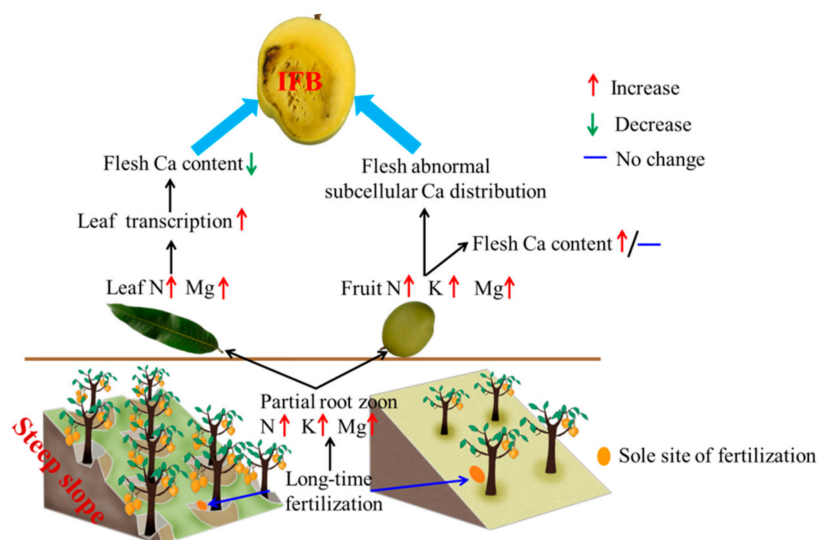


Figure 14. Speculative scheme of internal flesh breakdown development in mango fruit grown on the steep slope of a mountain.

5. Conclusions

IFB disorder was characterized by increased levels of N, P, K and Mg, and ratios of N/Ca, K/Ca and Mg/Ca in 'Keitt' mango fruit flesh. The correlation analysis showed that the IFB rate was correlated significantly with the N/Ca, K/Ca and Mg/Ca ratios. Ca deficiency was considered the major reason for IFB development in mango fruit, but our results showed that fruit flesh with IFB symptoms had high, low or similar Ca levels compared to the healthy fruit flesh. Hence, this research expanded our understanding of the causes of IFB in mango fruit flesh associated with calcium deficiency.

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