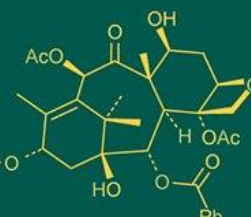
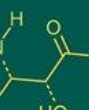
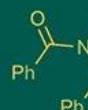


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Physiological response and spongy tissue dynamics of alphonso mango to ontogenetic plant growth regulator treatments in rejuvenated and non-rejuvenated orchard

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Abstract

Spongy tissue is one of the most serious internal physiological disorders limiting the marketability and export potential of Alphonso Mango, particularly under the humid coastal conditions of the Konkan region. The disorder is primarily associated with disturbed assimilate partitioning, impaired source-sink relationships, and metabolic imbalances during fruit development, resulting in localized mesocarp breakdown without external symptoms. Orchard rejuvenation, through canopy renewal and restoration of productive shoots, has the potential to improve canopy architecture, light interception, photosynthetic efficiency, and carbohydrate translocation, thereby enhancing fruit physiological processes and reducing the predisposition to spongy tissue formation. The present study investigated the physiological response and spongy tissue dynamics of Alphonso mango under rejuvenated and non-rejuvenated orchards subjected to ontogenetic plant growth regulator treatments during fruit development. Foliar application of KNO_3 at 1% during the pea, marble, and egg stages was evaluated for its influence on fruit physiology and disorder incidence. Rejuvenated trees exhibited improved source strength, more efficient assimilate allocation to developing fruits, and better sink activity than non-rejuvenated trees, leading to enhanced fruit growth and physiological stability. Among the treatments, KNO_3 (1%) applied at the critical ontogenetic stages in rejuvenated orchards significantly reduced the incidence of spongy tissue, likely through improved potassium-mediated assimilate transport, enhanced nitrogen metabolism, and maintenance of cellular integrity during rapid fruit enlargement. The findings demonstrate that integrating orchard rejuvenation with stage-specific KNO_3 application effectively modulates source-sink relationships and fruit physiological processes, providing a practical strategy for mitigating spongy tissue disorder and improving the productivity and fruit quality of Alphonso mango under Dapoli conditions.

Keywords: Spongy tissue, rejuvenation practice, alphonso, fruit physiology, heat convection

Introduction

'Alphonso' mango (*Mangifera indica* L.) is one of the world's most valued dessert mango cultivars because of its superior flavour, aroma, texture, and export quality. It is predominantly cultivated along the Konkan coast of Maharashtra, where the unique agro-climatic conditions contribute to its premium fruit quality and Geographical Indication status. However, its commercial production is severely constrained by spongy tissue, a major internal physiological disorder characterized by localized breakdown of the mesocarp without external symptoms, resulting in considerable postharvest losses and reduced market acceptability.

Spongy tissue is a multifactorial disorder influenced by genetic, environmental, nutritional, and physiological factors. Increasing evidence suggests that the disorder is closely associated with impaired assimilate partitioning, disrupted source-sink relationships, and metabolic imbalance during fruit ontogeny. Developing fruits act as strong sinks requiring a continuous supply of photoassimilates, mineral nutrients, and endogenous growth regulators from source leaves. Any disruption in assimilate production, phloem transport, or sink activity may restrict carbohydrate availability, alter cellular metabolism, and induce localized mesocarp degeneration, ultimately leading to spongy tissue formation.

Canopy architecture plays a critical role in regulating photosynthetic efficiency and carbon allocation. In senescent and overcrowded orchards, excessive shading and poor light interception reduce canopy photosynthesis, limit assimilate production, and weaken source-sink balance, thereby increasing the susceptibility of fruits to physiological disorders. Orchard rejuvenation through strategic pruning restores canopy structure, enhances light distribution, stimulates vigorous shoot growth, and improves carbon assimilation and assimilate translocation to developing fruits. These physiological changes strengthen fruit sink activity and may reduce the incidence of spongy tissue, although the underlying mechanisms remain inadequately understood.

Fruit growth in mango progresses through the pea, marble, and egg stages, which represent critical phases of cell division, expansion, and rapid assimilate accumulation. These ontogenetic stages determine sink strength and largely influence fruit quality and physiological stability. Potassium is a key regulator of phloem loading, carbohydrate translocation, osmotic adjustment, enzyme activation, and stomatal function, while nitrate supports nitrogen metabolism and photosynthetic capacity. Consequently, foliar application of potassium nitrate during these critical developmental stages may enhance source activity, improve assimilate partitioning, maintain cellular homeostasis, and reduce the risk of spongy tissue development.

Although foliar nutrient application and plant growth regulator treatments have been reported to improve mango fruit quality, limited information is available on their physiological interaction with orchard rejuvenation, particularly in relation to assimilate partitioning and spongy

tissue dynamics. Therefore, the present study investigated the physiological responses of rejuvenated and non-rejuvenated 'Alphonso' mango orchards to ontogenetic plant growth regulator treatments, with special emphasis on source-sink relationships, assimilate partitioning, and the role of stage-specific KNO₃ application in mitigating spongy tissue under the agro-climatic conditions of Dapoli.

Material and Methodology

Experimental site

The investigation was conducted during two consecutive mango cropping seasons (2023-24 and 2024-25) at the Department of Fruit Crops, Dr. Balasaheb Sawant Konkan Krishi Vidyapeeth, Dapoli, Maharashtra. The experimental orchard is located in the humid tropical coastal ecosystem of the Konkan region, which is characterized by high rainfall, moderate temperature, and lateritic soils, favouring commercial cultivation of 'Alphonso' mango.

Experimental Trees

A total of 84 uniformly grown 'Alphonso' mango trees, each 35 years old, were selected for the experiment. Trees were planted at a spacing of 10 m × 10 m and exhibited uniform canopy vigour and health. Based on canopy status, the trees were categorized into Rejuvenated orchard and Non-rejuvenated orchard. These two orchard conditions constituted the first experimental factor.

Experimental Design and Treatment Details

The experiment was conducted separately in rejuvenated and non-rejuvenated orchards using a Factorial Randomized Block Design with three replications during both experimental years.

Table 1: Experimental Factors

Factor A	Particulars
P ₁	Rejuvenated tree (35 year old)
P ₂	Non-Rejuvenated tree (35 year old)
Factor B	
C ₁	Salicylic Acid @1500 ppm (Peanut stage, Marble stage, Egg stage)
C ₂	Salicylic Acid @ 2000 ppm (Peanut stage, Marble stage, Egg stage)
C ₃	KNO ₃ @ 1% (Peanut stage, Marble stage, Egg stage)
C ₄	CPPU @ 3 ppm (Peanut stage, Marble stage, Egg stage)
C ₅	CPPU @ 4 ppm (Peanut stage, Marble stage, Egg stage)
C ₆	n-ATCA 10% and folic acid 0.2% @ 1 ml/L (50% Flowering), 1.5 ml/L (Marble stage) and 2 ml/L (Egg stage)
C ₇	Control

Table 2: Treatment combination

Treatment	Treatment Combination	Factor A X B
T ₁	P ₁ C ₁	Rejuvenated tree + Salicylic Acid @1500 ppm
T ₂	P ₁ C ₂	Rejuvenated tree + Salicylic Acid @ 2000 ppm
T ₃	P ₁ C ₃	Rejuvenated tree + KNO ₃ @ 1%
T ₄	P ₁ C ₄	Rejuvenated tree + CPPU @ 3 ppm
T ₅	P ₁ C ₅	Rejuvenated tree + CPPU @ 4 ppm
T ₆	P ₁ C ₆	Rejuvenated tree + n-ATCA 10% and folic acid 0.2% @ 1 ml/L (50% Flowering), 1.5 ml/L (Marble stage) and 2 ml/L (Egg stage)
T ₇	P ₁ C ₇	Rejuvenated tree + Control
T ₈	P ₂ C ₁	Non Rejuvenated tree + Salicylic Acid @1500 ppm
T ₉	P ₂ C ₂	Non Rejuvenated tree + Salicylic Acid @ 2000 ppm
T ₁₀	P ₂ C ₃	Non Rejuvenated tree + KNO ₃ @ 1%
T ₁₁	P ₂ C ₄	Non Rejuvenated tree + CPPU @ 3 ppm
T ₁₂	P ₂ C ₅	Non Rejuvenated tree + CPPU @ 4 ppm
T ₁₃	P ₂ C ₆	Non Rejuvenated tree + n-ATCA 10% and folic acid 0.2% @ 1 ml/L (50% Flowering), 1.5 ml/L (Marble stage) and 2 ml/L (Egg stage)
T ₁₄	P ₂ C ₇	Non Rejuvenated tree + Control

Orchard Management

Before initiation of the experiment, the orchard was cleaned during June by removing dead, diseased, weak, and crossing branches, followed by weed removal and sanitation. Farmyard manure and fertilizers were applied during the first week of August by placing them in circular trenches (30 cm wide and 15 cm deep) excavated at approximately half the canopy radius from the trunk. The recommended nutrient schedule consisted of Farmyard manure (FYM): 50 kg tree⁻¹, Nitrogen (N): 3.0 kg tree⁻¹, Phosphorus (P₂O₅): 3.0 kg tree⁻¹, Potassium (K₂O): 1.0 kg tree⁻¹. All other intercultural operations, irrigation, and plant protection measures were carried out according to the recommendations of Dr. Balasaheb Sawant Konkan Krishi Vidyapeeth, Dapoli, particularly for blossom and fruit protection against major pests and diseases.

Foliar Application of Plant Growth Regulators

Foliar sprays were imposed at critical ontogenetic stages of fruit development to evaluate their influence on fruit physiology and spongy tissue incidence. Treatments Applied at 50% flowering stage and various Fruit Developmental Stages that is Pea stage, Marble stage, Egg stage. All foliar sprays were applied uniformly using a foot-operated knapsack sprayer, ensuring complete coverage of the tree canopy during calm weather conditions.

Spongy tissue Occurrence

Spongy tissue occurrence percentage calculated by following formula:

$$\left[\frac{\text{No. of fruits exhibiting symptoms}}{\text{Total No. of fruits examined}} \times 100 \right]$$

Statistical Analysis

The experimental data collected during both cropping seasons were subjected to analysis of variance appropriate for a Factorial Randomized Block Design. Treatment means were compared using the Critical Difference test at the 5% level of significance ($P \leq 0.05$). Where appropriate, pooled analysis over years was performed to assess treatment consistency.

Physiological Basis of Spongy Tissue Development in 'Alphonso' Mango

Pea stage of fruit

The pea stage is characterized by active cell division, which determines the future sink strength and growth potential of developing 'Alphonso' mango fruits (Bangerth, 1989; Marcelis, 1996) [2, 13]. During this period, fruits act as strong metabolic sinks, importing carbohydrates, mineral nutrients, amino acids, and endogenous growth regulators from source leaves to support rapid cell proliferation and vascular development (Ho, 1988; Davies, 2010) [8]. Efficient source-sink relationships and assimilate partitioning at this stage are therefore essential for normal fruit development. Reduced canopy photosynthesis, inadequate potassium supply, and restricted vascular differentiation can impair assimilate translocation and weaken fruit sink activity (Lakso and Corelli Grappadelli, 1992; Cakmak, 2005; Marschner, 2012) [11, 4, 14]. Consequently, localized carbohydrate deficiency and metabolic imbalance develop within the mesocarp, predisposing fruits to tissue degeneration that later manifests as spongy tissue during fruit maturation and ripening (Bhatia *et al.*, 1967; Singh *et al.*, 2012) [3, 17].



Plate 1: Peanut stage of fruit development

Marble stage of fruit

The marble stage is a critical phase of fruit development in 'Alphonso' mango, characterized by rapid cell expansion, active xylem and phloem transport, and increased demand for photoassimilates and potassium to sustain fruit growth (Marcelis, 1996; Ho, 1988) [13, 8]. During this period, efficient assimilate partitioning from source leaves to developing fruits is essential for maintaining sink strength and normal mesocarp development. Any reduction in canopy photosynthesis or disruption in source-sink relationships restricts carbohydrate supply, resulting in localized carbon starvation within the fruit (Lakso and Corelli Grappadelli, 1992; Marcelis, 1996) [11, 13]. Potassium plays a vital role in phloem loading, sucrose transport, osmotic regulation, enzyme activation, and stomatal function; therefore, inadequate potassium availability reduces assimilate translocation and fruit growth (Marschner, 2012; Cakmak, 2005) [14, 4]. Elevated fruit temperature during this stage further accelerates respiration, increases carbohydrate consumption, and reduces net sugar accumulation, while excessive production of reactive oxygen species (ROS), including hydrogen peroxide (H₂O₂), superoxide radicals (O₂⁻), and hydroxyl radicals (OH[•]), induces oxidative damage to cellular membranes (Apel and Hirt, 2004; Gill and Tuteja, 2010) [1]. These physiological disturbances weaken mesocarp metabolism and predispose the fruit to the subsequent development of spongy tissue during maturation and ripening (Bhatia *et al.*, 1967; Singh *et al.*, 2013) [3, 17].



Plate 2: Marble stage of fruit development

Egg Stage

The egg stage is a critical phase of 'Alphonso' mango fruit development, characterized by rapid dry matter accumulation, maximum sink strength, and active import of carbohydrates for starch synthesis and fruit enlargement (Marcelis, 1996; Ho, 1988) [13, 8]. Efficient assimilate partitioning during this stage is essential for maintaining

mesocarp metabolism and normal fruit growth. Any reduction in phloem transport or source-sink efficiency limits sucrose import, resulting in localized carbohydrate depletion and metabolic starvation of mesocarp tissues (Ho, 1988; Marschner, 2012) [8, 14]. Increased respiratory activity further accelerates carbohydrate consumption, intensifying the imbalance between assimilate supply and demand (Taiz *et al.*, 2015) [18]. Simultaneously, excessive accumulation of reactive oxygen species (ROS) enhances membrane lipid peroxidation, leading to loss of membrane integrity and increased electrolyte leakage (Apel and Hirt, 2004; Gill and Tuteja, 2010) [1]. In addition, reduced activities of key carbohydrate-metabolizing enzymes such as invertase, sucrose synthase, and ATPase impair sugar metabolism and cellular energy production, thereby weakening mesocarp cells and predisposing them to spongy tissue development during fruit maturation and ripening (Singh *et al.*, 2013; Bhatia *et al.*, 1967) [3, 17].



Plate 3: Egg stage of fruit development

Harvest Stage

At harvest, 'Alphonso' mango fruits generally exhibit a normal external appearance despite the initiation of internal physiological changes associated with spongy tissue. By this stage, the disorder is already physiologically established in localized regions of the mesocarp, where reduced assimilate accumulation, poor starch reserves, membrane deterioration, and impaired metabolic enzyme activity have compromised cellular viability (Bhatia *et al.*, 1967; Singh *et al.*, 2013) [3, 17]. These metabolically weakened tissues remain symptomless externally but subsequently undergo abnormal ripening, resulting in the characteristic corky, unripe, and spongy patches observed during postharvest ripening (Bhatia *et al.*, 1967; Krishnamurthy *et al.*, 1971; Singh *et al.*, 2013) [3, 17].



Plate 4: Mature stage of Fruits

Ripening stage of fruit

During ripening, the physiological alterations initiated during fruit development become visibly expressed as spongy tissue. In healthy fruits, starch is hydrolysed into soluble sugars, cell wall-degrading enzymes facilitate pulp softening, and coordinated ethylene production ensures uniform ripening (Giovannoni, 2004; Taiz *et al.*, 2015) [6, 18]. In contrast, affected mesocarp tissues exhibit impaired starch degradation, reduced soluble sugar accumulation, abnormal ethylene-mediated ripening, and decreased activities of cell wall-modifying enzymes, resulting in hard, corky, and unripe patches within the pulp (Singh *et al.*, 2013) [17]. Concurrently, excessive reactive oxygen species (ROS) accumulation accelerates membrane lipid peroxidation, electrolyte leakage, and loss of cellular compartmentalization, ultimately leading to mesocarp collapse and the characteristic symptoms of spongy tissue (Apel and Hirt, 2004; Gill and Tuteja, 2010; Bhatia *et al.*, 1967) [1, 3].



Plate 5: Spongy tissue of Alphonso Ripe Fruits

Result and Discussion

Spongy Tissue Occurrence (%)

The data presented in Table 1. revealed that spongy tissue occurrence (%) of ripe Alphonso mango fruits was significantly influenced by different treatments. Alphonso mango is highly susceptible to the spongy tissue physiological disorder, which is primarily governed by its genetic makeup. In addition to genetic makeup of cultivar, environmental factors such as convective heat and high temperatures during fruit development play important role in the development of this disorder. Rejuvenation improves physiological efficiency and reduces incidence of disorders in old mango orchards Jadhav *et al.* (2021) [9].

With respect to factor A, treatment P₂ (non-rejuvenated tree) recorded the maximum spongy tissue incidence (6.69% during 2023-24 and 6.24% pooled), whereas the minimum was observed in P₁ (rejuvenated tree) (5.50%, 5.45% and 5.48% pooled). The differences were significant during 2023-24 and in pooled data, where P₁ was significantly superior (lower incidence) over P₂, while during 2024-25 the treatments were at par. Thus, P₁ proved effective in reducing spongy tissue and was followed by P₂.

In the factor B, the differences among treatments were statistically significant during both years and in pooled analysis. Treatment C₇ (control) recorded the maximum spongy tissue incidence (13.83% during 2023-24, 10.42% during 2024-25 and 12.13% pooled), followed by C₄ (6.33%) and C₂ (6.13%). The minimum incidence was

observed in C₃ (KNO₃ @ 1%) 1.58% during 2023-24, 2.25% during 2024-25 and 1.92% pooled, which was significantly superior in reducing spongy tissue, followed by C₆ (3.88%) and C₅ (5.17%). These treatments were statistically different from higher incidence treatments like C₇, indicating their effectiveness in minimizing the disorder. Physiological perspective, spongy tissue disorder is associated with impaired translocation of metabolites, heat stress, and oxidative damage within fruit tissues. Foliar application of KNO₃ (C₃) plays a crucial role in reducing this disorder by improving nitrogen metabolism, osmotic balance and membrane stability. Potassium enhances translocation of photosynthates and regulates enzyme activity, thereby preventing internal breakdown. Potassium

nutrition reduces spongy tissue incidence by improving pulp integrity and reducing physiological stress found by Ravishankar *et al.* (2018)^[15].

Regarding the interaction effect (A X B), significant differences were observed during 2023-24, while during 2024-25 and pooled data the treatments were non-significant. Numerically, the maximum spongy tissue incidence was recorded in P₂C₇ (15.67% during 2023-24 and 13.25% pooled). The minimum incidence was observed in P₁C₃ 1.00% during 2023-24 and 1.08% pooled. Similar result was found by Haldankar *et al.* (2019)^[7] and Malshe *et al.* (2022)^[12] who observed a decrease in spongy tissue incidence with foliar application of potassium nitrate in Alphonso mango under Konkan conditions.

Table 1: Effect of plant growth regulators on spongy tissue incidence (%) on mango fruits

	Treatment	Spongy tissue occurrence (%)		
		2023-24	2024-25	Pooled
Factor A (P)	P ₁	5.50	5.45	5.48
	P ₂	6.69	5.79	6.24
	Mean	6.10	5.62	5.86
	S.E. ±	0.26	0.35	0.25
	C.D. at 5%	0.76	NS	0.72
Factor B (C)	C ₁	5.42	5.50	5.46
	C ₂	5.75	6.50	6.13
	C ₃	1.58	2.25	1.92
	C ₄	6.58	6.08	6.33
	C ₅	5.50	4.83	5.17
	C ₆	4.00	3.75	3.88
	C ₇	13.83	10.42	12.13
	Mean	6.10	5.62	5.86
	S.E. ±	0.49	0.65	0.46
	C.D. at 5%	1.43	1.88	1.34
Factor (A X B)	P ₁ C ₁	6.00	5.83	5.92
	P ₁ C ₂	4.00	6.00	5.00
	P ₁ C ₃	1.00	1.17	1.08
	P ₁ C ₄	6.33	7.00	6.67
	P ₁ C ₅	5.67	4.00	4.83
	P ₁ C ₆	3.50	4.17	3.83
	P ₁ C ₇	12.00	10.00	11.00
	P ₂ C ₁	4.83	5.17	5.00
	P ₂ C ₂	7.50	7.00	7.25
	P ₂ C ₃	2.17	3.33	2.75
	P ₂ C ₄	6.83	5.17	6.00
	P ₂ C ₅	5.33	5.67	5.50
	P ₂ C ₆	4.50	3.33	3.92
	P ₂ C ₇	15.67	10.83	13.25
	Mean	6.10	5.62	5.86
	S.E. ±	0.69	0.91	0.65
	C.D. at 5%	2.02	NS	NS

NS: Non Significance

Factor A (P)	P ₁ -Rejuvenated tree (35 year old)	P ₂ -Non Rejuvenated tree (35 year old)
Factor B (C)	C ₁ -Salicylic Acid @1500ppm	C ₅ -CPPU @ 4%
	C ₂ -Salicylic Acid @2000ppm	C ₆ -n-ATCA @ 1ml/L (50% flowering), 1.5ml/L (Marble stage), and 2ml/L (Egg stage)
	C ₃ -KNO ₃ @ 1%	C ₇ -Control
	C ₄ -CPPU @ 3%	

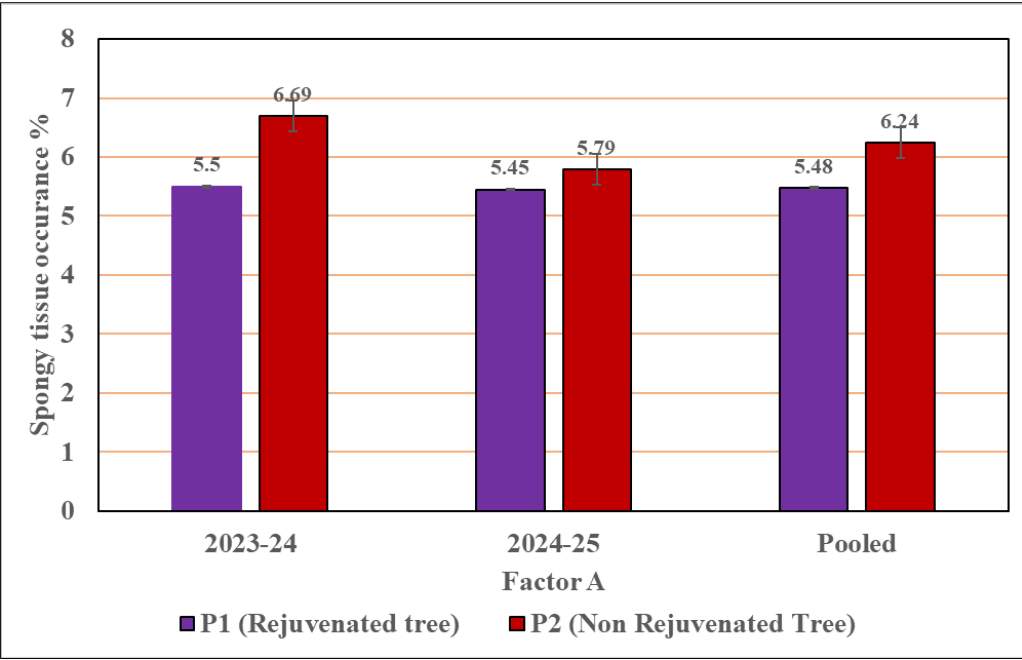


Fig 1: Effect of rejuvenation and non-rejuvenation on occurrence of spongy tissue in mango cv. Alphonso

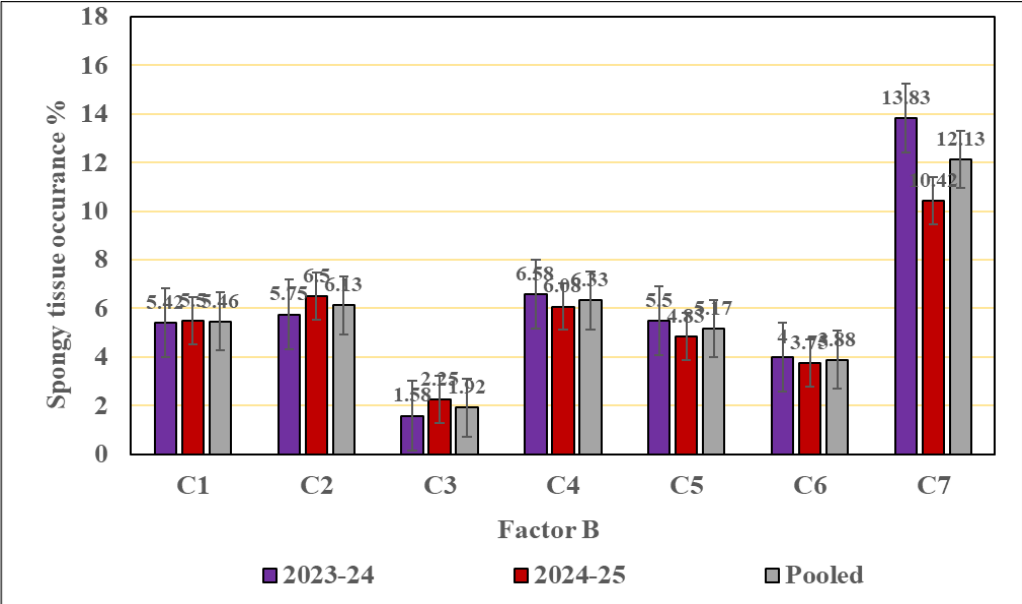


Fig 2: Effect of plants growth regulators on occurrence of spongy tissue in mango cv. Alphonso

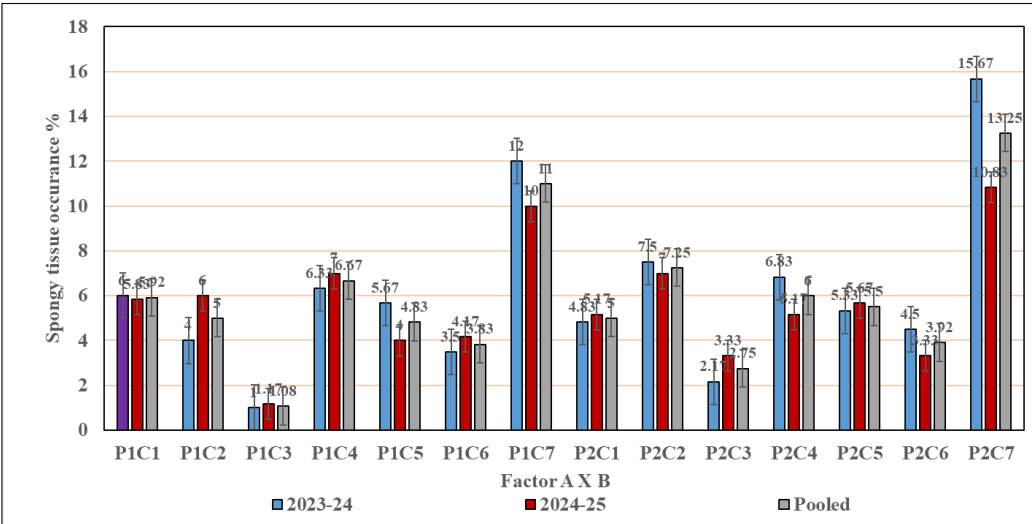


Fig 3: Interaction effect of rejuvenation practice and plants growth regulators on occurrence of spongy tissue in mango cv. Alphonso

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Conclusion

The present investigation demonstrated that both orchard rejuvenation and foliar application of plant growth regulators significantly influenced the incidence of spongy tissue in 'Alphonso' mango. Rejuvenated trees consistently exhibited lower spongy tissue incidence (5.48% pooled) than non-rejuvenated trees (6.24% pooled), indicating that canopy rejuvenation improves fruit physiological status and reduces susceptibility to internal breakdown. Among the foliar treatments, KNO_3 @ 1% (C_3) was the most effective, recording the lowest pooled spongy tissue incidence (1.92%), which was markedly lower than the control (12.13%). The interaction of rejuvenation with KNO_3 @ 1% (P_1C_3) produced the minimum spongy tissue incidence (1.08% pooled), demonstrating the synergistic effect of improved canopy architecture and potassium nutrition. The reduction in spongy tissue may be attributed to enhanced canopy photosynthesis, improved source-sink relationships, efficient assimilate partitioning, better potassium-mediated phloem transport, and maintenance of membrane integrity during fruit development. These physiological improvements likely reduced metabolic stress and prevented localized mesocarp degeneration associated with spongy tissue formation. Therefore, foliar application of KNO_3 @ 1% at critical fruit developmental stages in rejuvenated 'Alphonso' mango orchards can be recommended as an effective strategy for minimizing spongy tissue incidence and improving marketable fruit quality under the agro-climatic conditions of Dapoli.

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