Review

Tylenchulus semipenetrans-Induced Slow Decline of Citrus: Biochemical Mechanisms and Management Implications

Phatu W. Mashela * and Kgabo M. Pofu

Posted Date: 13 October 2025

doi: 10.20944/preprints202510.0892.v1

Keywords: dehydration avoidance; root-to-shoot ratio; salinity; slow decline of citrus; toxicity avoidance *Tylenchulus semipenetrans*

Preprints.org (www.preprints.org) | NOT PEER-REVIEWED | Posted: 13 October 2025 doi:10.20944/preprints202510.0892.v1

Review

Tylenchulus semipenetrans-Induced Slow Decline of Citrus: Biochemical Mechanisms and Management Implications

Phatu W. Mashela * and Kgabo M. Pofu

University of Limpopo, Green Biotechnologies Research Centre of Excellence, Private Bag X1106, Sovenga, 0727, Republic of South Africa
* Correspondence: phatu.mashela@ul.ac.za

Abstract

The slow decline of citrus is a complex syndrome primarily driven by the citrus nematode (*Tylenchulus semipenetrans*); with unexplained modulating influences from abiotic stressors such as soil salinity and nutrient imbalances. This review synthesises existing knowledge on the physiological and biochemical mechanisms underlying this progressive economic decline; focusing on the interplay between nematode infection; abrupt reduction in root-to-shoot ratio; and consequent osmolyte dynamics; along with management implications. The pruning effects of nematode females at death; result in abrupt diversion of the root-to-shoot ratio from the normal seasonal cycle; which triggers a series of dehydration- and ion-toxicity-avoidance mechanisms; where citrus trees redistribute hyperosmotic osmolytes; which involve chemical and physiological adjustments to restore the stable seasonal root-to-shoot ratio. This review underscores the importance of maintaining a stable seasonal root-to-shoot ratio through integrated management strategies. Avoiding mechanical weeding; while maintaining light shoot pruning; strategic fertilisation with potassium supplementation; improved irrigation management and selection of dual salt-tolerant and nematode-resistant-rootstocks are crucial for sustaining orchard longevity and productivity. By integrating the proposed strategies; citrus growers can improve tree longevity; maintain fruit production; and ensure long-term orchard sustainability. In conclusion; the review highlights the necessity of a holistic; multipronged management approach to mitigate the slow decline of citrus; with future research focusing on molecular pathways that govern the root-to-shoot homeostasis by exploring breeding strategies for citrus rootstocks with enhanced resilience against both biotic and abiotic stressors.

Keywords: dehydration avoidance**;** root-to-shoot ratio**;** salinity**;** slow decline of citrus**;** toxicity avoidance *Tylenchulus semipenetrans*

---

1. Introduction

The slow decline of citrus trees is a progressive disease syndrome primarily associated with infection by the citrus nematode, *Tylenchulus semipenetrans*. Worldwide, in citrus-producing regions this nematode is among the most economically devastating pathogens affecting citriculture, contributing to substantial citrus yield losses and reduced orchard longevity [1–3]. The symptoms of slow decline – stunted growth, leaf chlorosis, sparse foliage, small leaves, twig dieback and reduced fruit size, closely resemble those induced by salinity stress and nutrient element deficiencies, making diagnosis and management complex [4,5]. Several hypotheses have been proposed to explain the underlying mechanisms of slow decline, yet no single model fully accounts for its slow progressive nature overtime. Early studies suggested that *T. semipenetrans* induces nutrient element imbalances that were insufficient to explain the severity of stunted growth observed in infected citrus trees [6]. Others suggested carbohydrate depletion as a key driver, arguing that nematode-induced stress diverts energy resources away from shoot development, which was akin to the phenomenon observed in alternate fruit-bearing trees [7,8]. However, this explanation remains inadequate as slow decline lacks the cyclical fruit productivity patterns – the characteristic indicator of carbohydrate depletion in alternate fruit-bearing trees [9].

A pivotal shift in our understanding the complexity of the disease syndrome occurred when O'Bannon and Esser [10] proposed that nematode-induced membrane damage in roots facilitates the "sucking" of salinity ions (Cl^-, Na^+), leading to ion toxicity in leaves via the transpiration stream. The subsequent study expanded on this hypothesis, suggesting that *T. semipenetrans* infection disrupts the integrity of root membranes, altering ion transport and predisposing trees to osmotic stress [11]. More recent investigations have reinforced the view that slow decline is not exclusively a consequence of nematode infection but rather a complex interaction between biotic and abiotic stressors, particularly, osmoticum ions, soil salinity and *T. semipenetrans* infection [12–14]. Despite the empirically-based insights, there remains a critical gap in explaining how *T. semipenetrans* and abiotic factors interact to drive biochemical imbalances at the cellular level. This review aims to provide a comprehensive biochemical model of slow decline, expounding the interplay between nematode infection, hyper-osmotically active ions (Cl^-, Na^+, K^+) and non-structural carbohydrates. By identifying the mechanisms that drive the root-to-shoot ratio imbalances, particularly dehydration avoidance in root cells and ion toxicity in leaf cells, this review seeks to inform integrated management strategies that optimise citrus tree health, productivity, and orchard longevity.

2. Cyclic Nature of *Tylenchulus semipenetrans* Population Dynamics

The population dynamics of *T. semipenetrans* vary by region and environmental conditions, with some areas exhibiting no specific period of nematode population peaks [15], while others show one [16,17] or two peaks per year [4,16,18,19]. Understanding these nematode population fluctuations is essential for effective nematode management, as population surges often correlate with increased root damage and citrus decline. Several models have been developed to quantify nematode growth patterns, emphasising their density-dependent nature [20]. In plant-parasitic nematodes, population dynamics generally follow a density-dependent growth (DDG) pattern model, where nematode densities fluctuate in response to competition for infection sites, food availability, and environmental pressures [21]. The DDG patterns are usually expressed using quadratic relationships, as seen in most biological systems through the Curve-fitting Allelochemical Response Dose (CARD) algorithm computer model [22]. Failure to recognise the existence of DDG patterns have resulted in numerous inconsistent results in incidents linked to biochemical stressors [20]. Environmental stressors, particularly salinity fluctuations, play a crucial role in shaping *T. semipenetrans* population dynamics. Seasonal variations in soil salinity impact nematode survival and reproductive cycles, with high salinity levels reducing nematode mobility and juvenile hatch rates [23,24]. Conversely, leaching events that decrease soil salinity such as rainfall can facilitate nematode resurgence, creating cyclical population booms and declines [1,24]. These interactions highlight the complex interplay between abiotic stressors and nematode ecology.

Recent studies have also shown that population cycles of *T. semipenetrans* respond to biological management strategies. The use of biocontrol agents such as *Trichoderma harzinum*, cucurbitacin-based phytonematicides and certain synthetic chemical nematicides compounds have shown significant impacts on arresting nematode population dynamics, leading to predictable fluctuations in population densities [25]. Such findings underscore the importance of integrating nematode life cycle models into sustainable citrus management strategies to mitigate slow decline and therefore improving orchard longevity and productivity. Recent studies [26,27] have provided deeper insights into the cyclic population dynamics of *T. semipenetrans*, highlighting the influence of environmental factors and geographical variations. Understanding the elicitors for the patterns is crucial for developing effective management strategies to mitigate the impact of this test pest on citrus orchards. In a study conducted in Fasa, southern Iran, between 2018 and 2019 it was observed that *T. semipenetrans* populations exhibited two distinct peaks per annum [26]. The lowest nematode densities in both soil and roots occurred in July. In root populations, peaks were recorded in late May and November, while soil populations peaked in late May and December. The findings suggested the occurrence of two generations per year in that region. Similarly, a 2023 study in North Bihar, India, reported that nematode populations in soil and females per gram of roots were higher at a 30-cm soil depth when compared to the 20-cm soil depth throughout the year [27]. The populations peaked during May to June and August to September. Regression analysis showed a significant correlation between nematode numbers and soil temperature, with the maximum populations observed at temperatures from 25 to 29°C and the minimum from 9 to 12°C. These studies underscore the importance of environmental factors, particularly soil temperature and seasonal changes, in influencing the population dynamics of *T. semipenetrans*. Recognising these cyclic patterns in each hemisphere can inform the timing of management measures, such as the application of nematicides or cultural practices, to effectively manage nematode populations and reduce their detrimental effects on citrus production. This and other related information have enhanced our understanding of the cyclic nature of *T. semipenetrans* populations, emphasising the role of environmental conditions and hemispherical differences. Such knowledge is locally vital for developing targeted and timely management strategies to mitigate the impact of the citrus nematode on orchard health and productivity by ensuring that such peaks are at least suppressed to the minimum.

3. Cyclic Nature of Citrus Root and Shoot Flushes

Citrus trees exhibit a well-defined seasonal cyclic pattern of root and shoot flushes, which are sequentially regulated by both intrinsic and extrinsic factors. These seasonal biological patterns are essential for maintaining tree health, optimising nutrient uptake, and ensuring economic fruit production. The periodicity of root and shoot flushes is influenced by environmental conditions such as temperature, soil moisture, and biotic stressors, particularly the root pathogens and nematodes [14,28].

3.1. Seasonal Regulation of Root-to-Shoot Ratio

In most citrus-producing regions, root and shoot flushes occur as distinct but interdependent phases. The balance between root and shoot development is best explained by the concept of the root-to-shoot ratio, a biochemical equilibrium influenced by seasonal shifts. In citrus trees this ratio fluctuates from 1:4 to 1:2, where the higher ratio (1:4) favours shoot growth and development, whereas the lower ratio (1:2) supports root growth and development [14,29]. Temperature plays a critical role in dictating these seasonal directions and changes, with warm conditions typically stimulating shoot growth and cooler periods favouring root expansion [30]. However, untimely disruptions to the natural cycle, diverting the direction from the normal, can have detrimental consequences. Pests such as *T. semipenetrans* and *Phytophthora nicotianae* are known to affect root development, particularly during periods when the resources of the trees are directed towards shoot growth [30]. Nematode infection often leads to premature root senescence, with *T. semipenetrans* females at death, resulting in the pruning effect, all reducing the root-to-shoot ratio and impairing nutrient and water uptake. This shift inherently disrupt the allocation of hyper-osmotic chemical compounds, ultimately affecting the overall tree vigour and health [13].

3.2. Plant Responses to Root-to-Shoot Ratio Imbalances

The seasonal root and shoot flushes affect the root-to-shoot ratio, which can be visualised as a seasonal pendulum moving from the right (e.g. in favour of shoot flushes) through the equilibrium point to the left (e.g. in favour of root growth). Any abrupt external disruption to divert the seasonal direction of the root-to-shoot ratio, forces the plant to abruptly initiate corrective physiological responses, where the plant reallocates resources to the affected organ to restore the balance. For example, in split-root experiments, removing half the root system during an increasing root-to-shoot ratio phase induced a sharp decline in root mass, causing a compensatory reduction in shoot growth in favour of increasing root growth [13]. Remarkably, citrus seedlings were able to re-establish the normal root-to-shoot ratios within 14 days, highlighting the intrinsic agility of citrus trees to adapt to stress [31]. Similar adaptations were observed in mature citrus trees in Florida, USA, when the disruption was artificially induced through shoot pruning [32].

3.3. Management Strategies for Optimising Root and Shoot Flushes

Understanding the cyclic nature of citrus root and shoot flushes provides valuable insights for orchard management. The timing of cultural practices such as fertilisation, irrigation, and light shoot pruning should align with the root-to-shoot ratio natural cycles to support optimal tree growth. For instance, applying nitrogen fertilisers at the inception of shoot flushes can enhance vegetative growth, while the inception of root flushes requires adequate soil moisture and nutrient availability for sustained root expansion [14]. Additionally, biological and chemical management measures for nematode and fungal infections should be strategically implemented to minimise disruptions to root development. Research has shown that managing nematode populations through biocontrol agents such as *Trichoderma* species or chemical nematicides can help maintain a stable root system, reducing repeated fluctuations in the root-to-shoot ratio [25,26].

4. *Tylenchulus Semipenetrans*-Salinity Interactions

Tylenchulus semipenetrans infection incidentally disrupts root functions, leading to reduced water and nutrient uptake, resulting in tree decline and unsightly appearance with decreased fruit yield [1,3]. Among the environmental factors influencing *T. semipenetrans* population dynamics, salinity plays a critical role, altering nematode mobility, second-stage juveniles (J2) hatch, and pathogenicity. Salinity levels in the soil can fluctuate due to irrigation practices, water quality,, and high evapotranspiration, all inducing cyclic salinity patterns that affect nematode populations differently when compared to constant salinity stress [24]. This review explores how cyclic salinity influences the population density of *T. semipenetrans*, providing insights into its adaptive strategies and implications for citrus orchard management.

4.1. Understanding Salinity Stress and Its Effects on Nematodes

4.1.1. Types of Salinity Stress in Soils

Soil salinity is a condition where the accumulation of soluble salts, particularly sodium (Na^+), chloride (Cl^-), calcium (Ca^{2+}) and magnesium (Mg^{2+}) ions in the rhizosphere, significantly impact plant health and soil microbial communities, including nematodes [5,33,34]. Salinity stress in citrus orchards can occur in two primary forms, namely, continuous or cyclic salinity [24]. Continuous salinity occurs when high salt concentrations persist in the soil due to poor drainage, improper irrigation, natural soil conditions or continuous irrigation with poor quality water. In contrast, cyclic salinity occurs when salinity levels fluctuate over time due to irrigation with saline water followed by leaching events (rainfall or fresh-water irrigation), mimicking natural best irrigation practices. Nematodes, including *T. semipenetrans*, respond differently to these two forms of salinity stress. Continuous salinity tends to suppress nematode populations by directly affecting their bioactivities including but not limited to mobility and egress, whereas cyclic salinity inevitably creates favourable conditions for population surges and pronounced damage [24].

4.1.2. Influence of Cyclic Salinity on *Tylenchulus semipenetrans* Population Density

In this review, the influence of cyclic salinity on *T. semipenetrans* was limited to three cases, as outlined below:

4.1.2.1. Effect on J2 Hatching and Mobility

Salinity stress impacts the ability of *T. semipenetrans* J2 to move through soil and locate host roots. Studies have shown that high osmotic pressure in saline soil reduces juvenile mobility and egress from egg masses, thereby delaying infection of new roots [35–37]. However, under cyclic salinity conditions, these effects are reversible. When saline soils are leached with freshwater, nematode mobility and J2 hatching rates recover rapidly, leading to sharp increases in population density [24]. This explains why citrus orchards experiencing seasonal fluctuations in salinity often exhibit steep cyclic patterns of nematode population density infestations.

4.1.2.2. Impact on Reproduction and Life Cycle Progression

Cyclic salinity affects the reproductive efficiency of *T. semipenetrans* in complex ways. High salinity initially suppresses egg production, J2-hatch and development and mobility, collectively causing nematode population declines. During fresh-water irrigation or any drainage events, nematodes recover, leading to population spikes as reproductive activity resumes [48]. This pattern results in two or more peaks in nematode population density per year, corresponding to seasonal salinity fluctuations. Similar observations were reported on various nematodes in Texas [23], on *T. semipenetrans* in Florida [38,39] and in South Africa [12], where citrus orchards with fluctuating salinity levels exhibited more pronounced nematode population cycles when compared to consistently saline or non-saline conditions.

4.1.2.3. Physiological Adaptation of *Tylenchulus semipenetrans* to Salinity

Nematodes exhibit various forms of cryptobiosis adaptation, where they enter undetectable metabolic state in response to various abiotic stressors, including high salinity stress, when it is gradually introduced [40]. In cryptobiosis state metabolic activities decrease, reducing energy consumption; with the cuticle thickening, thereby increasing tolerance to osmotic stress. Additionally, egg masses become more tolerant to environmental extremes, allowing nematode populations to persist in such unfavourable conditions. But, once salinity stress is relieved through dilution (rainfall or freshwater irrigation), affected various nematode stages exit the cryptobiosis state and resume normal bioactivities, leading to a sudden increase in infection rates and population density [23]. Three examples of implications for citrus management with respect to the influence of cyclic salinity on *T. semipenetrans* population density are enlisted.

4.1.2.3.1. Irrigation Practices and Salinity Management

Cyclic salinity poses challenges for managing *T. semipenetrans* populations because nematodes can exploit periods of reduced salinity for rapid population recovery. To minimise nematode outbreaks, the grower needs to prevent cyclic salinity through one of three strategies: (a) monitor irrigation water quality to prevent excessive salt accumulation, (b) use scheduled leaching events to flush out excess salts while avoiding conditions that promote nematode resurgence, and (c) adopt alternative irrigation methods such as drip irrigation, which reduce salt build-up while maintaining adequate soil moisture in the target rhizosphere [24].

4.1.2.3.2. Biological and Chemical Management Strategies

Managing *T. semipenetrans* in saline conditions requires a combination of approaches, which may include but not be limited to combining synthetic chemical nematicides, biocontrol agents such as *Trichoderma* species and phytonematicides. Salinity can interfere with the effectiveness of synthetic chemical nematicides and biocontrol agents. Studies suggest that phytonematicides based on cucurbitacins can suppress nematode populations while minimising environmental interferences [25]. Additionally, using salt-tolerant rootstocks such as Cleopatra mandarin and Rangpur lime could enhance salt tolerance, although such rootstocks are highly susceptible to *T. semipenetrans* infection, with high infections resulting in loss of salt tolerance [12,13].

4.1.2.3.3. Soil and Nutrient Management

Maintaining proper soil health can mitigate the effects of salinity and nematode infection. For example, growers can increase potassium levels since potassium counteracts the toxic effects of

Preprints.org (www.preprints.org) | NOT PEER-REVIEWED | Posted: 13 October 2025 doi:10.20944/preprints202510.0892.v1

sodium and helps maintain osmotic balance in citrus trees [41]. Additionally, growers should enhance soil organic matter, which improves soil structure, reduces salt accumulation, and supports beneficial microbial communities that suppress nematodes [1]. Fouche *et al*. [52] observed that if population densities of *T. semipenetrans* were above the economic damage threshold, citrus trees were not responding to potassium fertilisation, which is addressed later in this review.

4.2. Influence of Salinity on Nematode Resistance in Citrus Rootstocks

Citrus rootstocks play a crucial role in determining tree vigour, fruit yield, and tolerance to environmental stressors, including nematode infection and soil salinity [41]. However, a growing body of knowledge suggests that salinity can compromise the resistance of some rootstocks to *T. semipenetrans*, exacerbating the slow decline symptoms and loss of orchard productivity [13]. Understanding the interplay between salinity stress and nematode resistance is essential for developing integrated management strategies for sustainable citrus production. Highly nematode-resistant commercial rootstocks, such as trifoliate orange (*Poncirus trifoliata*) and its hybrids - including but not limited to Swingle citrumelo (*Citrus paradisi* × *P. trifoliata*), Carrizo citrange (*C. sinensis* × *P. trifoliata*), and Troyer citrange (*P. trifoliata* × *C. sinensis*) – are known to be sensitive to salinity stress [41]. Studies suggest that salt stress can disrupt physiological defense mechanisms in these rootstocks, making them more susceptible to *T. semipenetrans* infection [30,46]. This phenomenon occurs because salinity alters root exudates, potentially enhancing nematode attraction, feeding and then reproduction. Mashela *et al*. [43] demonstrated in pot experiments that cyclic salinity increased *T. semipenetrans* egg production by two- to tenfold across different nematode-resistant citrus rootstocks. Basically, the overall ranking of rootstock resistance remained unchanged, while nematode populations proliferated under saline conditions, leading to greater root damage and tree stress. Similarly, field observations have confirmed that high nematode densities and severe slow decline symptoms are most prevalent in citrus-growing regions with elevated soil salinity [2,3]. Recent research has further elaborated on these interactions. Duncan [42] reported that fluctuating salinity levels – especially seasonal transitions from high to low salinity, can create conditions favourable for nematode reproduction. Conversely, citrus trees growing in sandy soils with low organic matter often exhibit suppressed nematode populations, suggesting that soil composition plays a critical role in modulating nematode resistance under saline conditions.

4.3. Mechanisms of Salinity-Induced Susceptibility

The interaction between *T. semipenetrans* and soil salinity presents significant challenges in citrus production, particularly concerning the efficacy of nematode-resistant rootstocks. Research indicates that elevated salinity levels can compromise the resistance of certain citrus rootstocks to *T. semipenetrans*, leading to increased nematode reproduction and associated plant health issues. In Florida, USA, Mashela *et al.* [24] examined the impact of salinity on six citrus rootstocks with varying resistance levels to *T. semipenetrans*. Results showed that salinity increased nematode egg production by two to tenfold across all rootstocks, though the relative resistance rankings among the rootstocks remained unchanged. This suggests that while salinity exacerbates nematode proliferation, it does not alter the inherent resistance hierarchy among different rootstocks. Further research in central and south-eastern Florida by Duncan *et al*. [30] highlighted that high densities of *T. semipenetrans* and the manifestation of slow decline symptoms are prevalent in citrus-producing areas with elevated salinity. This correlation underscores the compounded stress that salinity and nematode infestation impose on citrus trees, leading to significant declines in fruit yield and overall tree vitality.

The mechanisms underlying the influence of salinity on nematode resistance are multifaceted. Salinity-induced osmotic stress can weaken the defense systems in trees, making them more vulnerable to nematode invasion. Additionally, salinity may alter root exudate composition, potentially enhancing nematode attraction and reproduction [1]. The findings have practical implications for citiculture in saline environments. Additionally, certain rootstocks exhibit resistance to *T. semipenetrans*, while their effectiveness can be diminished under high salinity. Therefore, managing soil salinity is crucial to maintain the efficacy of resistant rootstocks. Integrating salinity management practices with the selection of appropriate rootstocks can help mitigate the adverse effects of both salinity and nematode infestation, ensuring sustainable citrus production. The interplay between *T. semipenetrans* and soil salinity significantly impacts the resistance of citrus rootstocks. Elevated salinity levels can compromise rootstock resistance, leading to increased nematode reproduction and associated plant health issues. Effective management strategies should focus on managing soil salinity and selecting suitable rootstocks to mitigate these challenges.

Recent studies have further elucidated the complex interactions between *T. semipenetrans* and soil salinity, particularly concerning the influence of salinity on the resistance of citrus rootstocks. These insights are crucial for developing effective management strategies in citrus cultivation. Duncan [45] highlighted that the fluctuations in soil salinity, especially transitions from high to low salinity, can favour nematode reproduction. Conversely, sandy soils with low organic matter content tend to hinder nematode population increases. This suggests that soil composition and salinity dynamics play significant roles in nematode proliferation. Verdejo-Lucas *et al*. [3] emphasised the ongoing need to develop new citrus rootstocks that are well-adapted to specific regional conditions and tolerant to various stressors, including salinity and nematode infestations. The research by Verdejo-Lucas *et al*. [3] focused on screening hybrid citrus rootstocks for resistance to *T. semipenetrans*, aiming to identify varieties that can maintain resistance even under salt conditions. Their findings underscore the importance of considering both intrinsic plant resistance and extrinsic environmental factors in managing *T. semipenetrans* population density. Worldwide, developing and selecting rootstocks that can withstand salinity-induced stress while maintaining nematode resistance is essential for sustainable citrus production. Sufficient research evidence indicates that soil salinity can significantly impact the resistance of citrus rootstocks to *T. semipenetrans* [24]. Fluctuating salinity levels inherently enhance nematode reproduction, while certain soil compositions can mitigate this effect. Ongoing efforts to develop and select appropriate rootstocks are vital for effective management of nematode infestations in saline environments.

4.4. Influence of Nematode Infection on Salt Tolerance

Citrus rootstocks play a vital role in mitigating abiotic stressors such as soil salinity, which can severely impact tree health and productivity. Certain commercial rootstocks, including Cleopatra mandarin (*Citrus reticulata*) and Rangpur lime (*C. reticulata* var. austere Swingle), are widely recognised for their salt tolerance. However, these rootstocks are highly susceptible to *T. semipenetrans* infection, which can severely compromise their ability to withstand saline conditions [25,46]. The interaction between nematode infection and salinity stress exacerbates physiological imbalances in citrus trees, accelerating symptoms of slow decline and reducing overall orchard productivity. The ability of salt-tolerant citrus rootstocks to exclude Na^+ and Cl^- ions from leaves is a key determinant of their salt tolerance [34,47]. However, infection by *T. semipenetrans* disrupts this exclusion mechanism, leading to increased ion accumulation in leaf tissues, which in turn causes toxicity and leaf abscission [13,41]. This breakdown of salt tolerance in infected rootstocks is attributed to several physiological and biochemical alterations, with three being provided as examples.

4.4.1. Reduced Root-to-Shoot Ratio and Osmotic Imbalances

Root pruning effects caused by *T. semipenetrans* infection females at death lead to a significant reduction in root biomass, lowering the root-to-shoot ratio [13]. The reduction in root mass impairs the plant's ability to maintain osmotic balance, resulting in excessive accumulation of osmolytes (Cl^-, Na^+) in leaves, leading to phytotoxicity [14]. Infected trees exhibit a decline in K^+ levels, since K^+ is displaced from root tissues to leaf tissues, but ultimately retuned to roots for catalysis of starch synthase. Unfortunately, just to be exuded into soil solutions to enhance hydration avoidance in root cells, which further aggravates slow decline symptoms [12,46].

4.4.2. Increased Susceptibility to Ion Toxicity and Dehydration Avoidance Mechanisms

Increased accumulation of Na^+ and Cl^- ions in leaf tissues disrupts cellular functions, reducing photosynthesis and promoting premature leaf senescence prior to abscission [48,49]. As a compensatory response, affected citrus trees initiate dehydration avoidance mechanisms in roots which drive an increased flux of hyper-osmotically active ions from roots to leaves, with the return of K^+ to roots worsening the toxicity effects [50]. The abscission of leaves as avoidance to ion toxicity, which leads to sparse canopies, poor fruit development, and a progressive decline in tree vigour, which are inherent characteristics of the slow decline syndrome [13].

Several studies have demonstrated the interaction between nematode infection and salt tolerance in commercial citrus rootstocks. Mashela *et al.* [24] conducted management led experiments under the greenhouse in Florida, which showing that T. *semipenetrans* infection significantly increased Na^+ and Cl^- concentrations in citrus leaves while depleting K^+ levels in both roots and leaves. The severity of these changes correlated with the reductions in root-to-shoot ratios. Duncan *et al.* [30] observed that citrus orchards in saline regions of Florida with high nematode populations exhibited accelerated tree decline, smaller fruit sizes, and reduced yield compared to non-infested but similarly saline-affected orchards. Studies on various rootstocks have shown that while some rootstocks effectively exclude salinity ions under non-infected conditions, their salt tolerance collapses when nematode infection compromises the root-to-shoot ratio [13]. These findings confirm that nematode infestation undermines the physiological mechanisms that allow salt-tolerant rootstocks to thrive in high-salinity environments, making them vulnerable to both nematode damage and ion toxicity.

4.4.3. Implications for Citrus Management in Orchards on Salt-Tolerant Rootstocks

Given the detrimental effects of *T. semipenetrans* on salt-tolerant rootstocks, an integrated management strategy is essential to sustain citrus production in saline environments. The strategy could include but not be limited to (a) selecting dual-tolerant rootstocks through rootstock breeding programmes that focus on developing hybrids that combine nematode resistance with salt tolerance [3]. Advanced screening techniques should identify genotypes capable of maintaining ion exclusion mechanisms even under nematode infection stress, (b) optimising soil and irrigation management by implementing management-led irrigation and leaching programmes that can reduce salt accumulation without triggering nematode population surges [24], (c) using soil amendments such as active biochar, organic matter or gypsum to improve soil structure and minimise salt build-up [51], (d) using integrated nematode management strategies that include the use of phytonematicides such as cucurbitacin-based products which can effectively reduce *T. semipenetrans* populations without disrupting soil microbial communities [21,25]. Additionally, biological management agents, including antagonistic fungi and bacteria, should be explored as eco-friendly alternatives to conventional synthetic chemical nematicides. Also, (e) maintaining optimal root-to-shoot ratios through using pruning strategies should be adjusted to favour shoot pruning over root pruning, as excessive root loss exacerbates nematode-induced stress [13], along with (f) prioritising K^+ supplementation fertilisation regimes to counteract nematode-induced K^+ depletion and improve ion balance. For the reasons already advanced under dehydration avoidance mechanisms, Fouche *et al.* [52] observed that citrus under field conditions with high nematode numbers could hardly respond to K fertilisation until the nematode populations were reduced to below the economic threshold levels

5. Tree Adaptation to Reduced Root-to-Shoot Ratio

Citrus trees exhibit extraordinary resilience to changes in their root-to-shoot ratios, a critical factor influencing their growth, resource allocation, and overall but unusual adaptability. An abrupt reduction in root-to-shoot ratio, where root biomass is disproportionately lower than the shoot biomass, can result from various environmental stressors that include nutrient deficiencies, drought, and elevated temperatures (Table 1). Recent research has shed light on the tree mechanisms employed to cope with such disruptions, with three examples given to explain this point.

Table 1. Abiotic and biotic factors which accelerate *Tylenchulus semipenetrans*-induced slow decline of citrus.

Elicitor	**R/S ratio**	**Cl**		**Na**		**K**		**References**
		root	**leaf**	**root**	**leaf**	**root**	**leaf**	
Biotic effects								
Tylenchulus semipenetrans	D	D	I	D	I	D	D	1,5,12,52
Phytophthora citrophilus	D	D	I	D	I	D	D	5
Mycorrhiza	D	D	I	D	I	D	D	5
Abiotic effects								
Salinity	D	D	I	D	I	D	D	5,13,34,41,47,51
Drought	D	D	I	D	I	D	D	41
Salt type	D	D	I	D	I	D	D	34
RT pruning	D	D	I	D	I	D	D	29
ST pruning	I		D	D	D	I	I	32,56

D and I imply that the elicitor decreased and increased the test variable, respectively.

5.1. Adaptations to Nutrient Deficiencies

Nutrient scarcity, particularly of N and P, significantly impacts the root architecture and biomass allocation. A comprehensive meta-analysis revealed that under N and P deficiencies, plants often exhibit a decrease in total root length and biomass. However, there is an increase in the root-to-shoot ratio and root length per unit of shoot biomass, indicating a strategic reallocation of resources to enhance nutrient uptake efficiency. This adjustment underscores the ability of a plant to modify its growth patterns in response to nutrient limitations.

5.2. Responses to Drought Conditions

Drought stress prompts trees to alter their biomass distribution to optimise water acquisition. Species adapted to arid environments typically develop higher root-to-shoot ratios and deeper root systems compared to those in more mesic conditions. This increased root investment facilitates access to deeper soil moisture, enhancing drought resilience. A meta-analysis of forest and woodland species demonstrated a significant increase in root-to-shoot ratios with decreasing annual precipitation, highlighting the adaptive significance of root system modifications in water-limited environments.

5.3. Impact of Elevated Temperatures

Climate change-induced temperature rises affect root development and biomass allocation. Elevated soil temperatures can lead to a reduction in root growth, including shorter primary roots and inhibited lateral root formation. Consequently, the root-to-shoot ratio decreases due to diminished carbon allocation to roots. This shift can compromise the ability of plants to absorb water and nutrient elements, potentially affecting overall growth and productivity.

6. Mechanisms Underlying Adaptation to Reduced Root-to-Shoot Ratios

The trees employ a wide range of adaptive strategies to reduced root-to-shoot ratios, with three examples provided as an illustration.

6.1. Biomass Reallocation

In response to environmental stressors, trees may adjust biomass distribution, allocating more resources to root growth and development to enhance water and nutrient uptake. This reallocation is crucial for maintaining physiological functions under adverse conditions, especially when the root-to-shoot ratio is diverted from the normal seasonal cycles. However, repeated diversions from the normal seasonal cycles when the female nematodes die could eventually reach critical threshold of no return, where the tree dips into the zone of slow decline to slow down the normal physiological activities.

6.2. Root Morphological Changes

Alterations in root architecture, such as increased root hair length and density, can improve the root surface area, facilitating better absorption of water and nutrients as observed in root pruning studies. These morphological adaptations are vital in combating environmental stresses, including the root pruning effects of female nematodes at death.

6.3. Physiological Adjustments

Changes in physiological processes, including modulation of hormone levels like auxins, play a role in root development and adaptation. These adjustments help trees to maintain growth and function despite reduced root biomass and managing the elicitors can help the tree to succeed in its fightback adjustment.

7. Cellular Responses to Forced Reduction in Root-to-Shoot Ratios

The root-to-shoot ratio is a fundamental equilibrium in plant physiology, ensuring the coordinated allocation of resources between roots and shoots. Any reduction that diverts this ratio from its normal seasonal cycle, such as those caused by *T. semipenetrans* females at death , root pruning, or environmental stressors like salinity and drought spells, all trigger a series of intrinsic cellular responses aimed at restoring optimum homeostasis. These responses primarily involve osmotic adjustments, metabolic reprogramming, and ion redistribution, which collectively determine the plant resilience and overall tree health [13,53]. Due to the importance of cellular responses, several examples were used to illustrate the point.

7.1. Osmotic Adjustments in Root Cells

Almost always, when the root-to-shoot ratio is reduced, an excess of photosynthates, primarily sucrose, is translocated from leaf to root tissues. This sudden influx of sucrose into root cells creates a hypoosmotic environment, leading to increased water influx into root cells due to reduced osmotic potential. The resulting elevated turgor pressure exerts mechanical stress on cellular organelles, particularly those with single or double-layered membranes [28]. To mitigate the risk of the organelles succumbing to damage induced by turgor pressure, root cells implement three primary osmotic adjustment mechanisms, namely:

7.1.1. Sucrose Hydrolysis and Starch Biosynthesis

Excess sucrose in root cells is hydrolysed into glucose and fructose, which are either used in metabolism or converted into non-osmotic starch for storage. This reduces the osmotic potential, alleviating the influx of water into root cells and therefore reducing the turgor pressure within root cells [13].

7.1.2. Ion Redistribution

Hyperosmotic ions such as Cl^-, Na^+ and K^+ ions are actively mobilised from root cells to leaf tissues via the transpiration stream. This movement serves a dual purpose of relieving osmotic stress in root cells and ensuring that excessive ion accumulation in cytoplasmic spaces does not collapse cellular functions [28,50]. Under normal conditions when the root-to-shoot ratio is synchronised with its normal seasonal cycle of the root-to-shoot ratio, citrus trees maintain a high concentration of Na^+

and Cl^- ions in root tissues while keeping such ions lower in leaf tissues [13,43]. In contrast, K^+ levels are kept higher in both leaf and root tissues. However, when the root-to-shoot ratio is compromised, the normal partitioning of the hyperosmotic ions ins is disrupted, leading to their abnormal accumulation in both leaf and root tissues [13]. The process unfolds in several distinct steps, which include but are not limited to the following:

7.2.1.1. Displacement of Ions from Root Cells

The reduction in root mass triggers the movement of high concentrations of hyperosmotic sucrose molecules into root cells, which displaces hyperosmotic ions (Na^+, Cl^-, K^+) from root cells into the apoplastic space, in attempts to regulate turgor pressure in root cells induced by water influx [13]. The displaced ions enter the xylem vessels, where they are then transported to leaf tissues via the transpiration stream [54].

7.2.1.2. Accumulation of ions in leaf tissues and ion toxicity avoidance

Once in the leaves, the hyperosmotic ions accumulate in the mesophyll cells, with Cl^- and Na^+ eventually reaching toxic levels at 0.10% and 0.25%, respectively [55], above which ion toxicity ensues. Eventually, the affected leaves are abscised, thereby offloading the toxic ions from the tree – a process referred to as ion toxicity avoidance mechanism. This process, while protective, results in sparse foliage and reduced photosynthetic capacity – a characteristic of slow decline in citrus trees. Unfortunately, the fallen toxic leaves within the dripline, further contribute to salinity challenges during decomposition [43].

7.2.1.3. Redeployment of K+ ions to roots and excretion to soil solution

Potassium ion, which is essential for enzymatic activation, is promptly remobilised back to roots to promote catalysis of starch synthase, which converts glucose to starch – a non-osmotic carbohydrate [56]. But due to the continued influx of hyperosmotic sucrose, the return of K^+ ions to root cells counter the desired effects of redeploying K^+ from leaf to root tissues, with the resultant excretion of K^+ ions from roots into soil solution, further depleting plant K^+ reserves in the affected trees [12,31]. Sucrose, as a non-polar sugar molecule cannot be excreted through the cell membranes into soil solution.

7.2.1.4. Complimentary processes to dehydration avoidance mechanism

The physiological responses induced by the reduced root-to-shoot ratios extend beyond osmotic imbalances, ion displacement and ion toxicity avoidance mechanism. Additionally, dehydration avoidance mechanism induces several other critical metabolic shifts to support the survival of trees under stress conditions, which include but may not be limited to the following:

7.2.1.4.1. Regulation of enzymatic activity

Potassium ions play a critical role in catalysing starch synthase, the enzyme responsible for converting glucose into starch as part of osmoregulation. However, when K^+ is displaced from root tissues into soil solutions, starch synthesis is inhibited, leading to inefficient carbohydrate storage for subsequent utilisation [28,50], triggering hormonal activities

7.2.1.4.2. Alteration in Hormonal Signalling

A decrease in the root-to-shoot ratio alters auxin and cytokinin levels, which are critical for regulating root and shoot growth balance [57]. The reduction in cytokinin production from roots results in premature leaf senescence and abscission, further exacerbating the decline in tree vigour [46]. Generally, citrus trees employ a complex hormonal signalling network to regulate dehydration responses, involving but not limited to ABA which triggers stomatal closure and enhances root growth to improve water uptake [14]. Auxins and cytokinin concentrations decline under root stress, reducing shoot growth to balance the root-to-shoot ratio [57]. Also, the accumulation of ethylene in leaves promotes leaf abscission, while the accumulation of jasmone acid enhances antioxidant defences to counteract oxidative stress from ion toxicity as K is exuded [46]. Certain advancements in citrus breeding have focused on selecting rootstocks with enhanced hormone-mediated drought tolerance, thus, improving resilience to dehydration stress [3].

7.2.1.4.3. Inhibition of Water Retention Mechanisms

Under conditions of reduced root-to-shoot ratio, as the tree attempts to compensate for root loss, increased leaf transpiration rates lead to further dehydration stress. This cycle reinforces the osmotic imbalance, worsening slow decline symptoms and impairing fruit development [13].

7.2.1.4.4. Active Ion Compartmentalisation

Upon exposure to hydration avoidance conditions, to assist in regularising water efflux, the root cells often increase the net uptake of inorganic ions. This process aids in osmotic adjustment by lowering the osmotic potential, thereby retarding water influx and maintaining a balanced turgor pressure. For instance, studies on *Arabidopsis thaliana* root epidermal cells demonstrated that hyperosmotic stress significantly enhances the uptake of K^+, Cl^-, and Na^+ ions, contributing to rapid turgor recovery. This ion accumulation is primarily mediated by voltage-gated transporters at the plasma membrane, allowing for swift osmotic balance restoration. During such uptakes, Na^+ can be beneficial for immediate osmotic adjustment, with excessive accumulation posing a risk of ion toxicity to the cytoplasm organelles. To mitigate this, plants compartmentalise Na^+ into vacuoles, sequestering it away from the cytoplasm and thus preventing interference with a wide range of essential cellular processes. This compartmentalisation not only aids in osmotic balance but also protects metabolic functions from the detrimental effects of high Na^+ concentrations.

7.2.1.4.5. Role of Organic Osmolytes

In addition to inorganic ions, plants synthesise a wide range of organic osmolytes such as proline, glycine betaine, and soluble sugars that contribute to osmotic adjustments. These compounds are highly soluble and non-toxic to plant cells, being allowed to accumulate to high concentrations without disrupting cellular functions. The organic osmolytes play a crucial role in stabilising proteins and cell membranes under stress conditions in addition to complementing the osmotic functions of inorganic ions. Ordinarily, the outlined strategic accumulation of both inorganic ions and organic osmolytes enables plants to effectively manage osmotic stress. By fine-tuning the uptake and compartmentalisation of hyperosmotic active ions and solutes, plants maintain cellular hydration and turgor pressure, ensuring continued growth and survival under adverse environmental conditions induced by interruptions to the normal seasonal root-to-shoot ratio. In this instance, the organic osmolyte balance is critical, as excessive reliance on inorganic ions without proper compartmentalisation can invariably lead to cytotoxicity, while sole dependence on organic osmolytes may not provide sufficient osmotic adjustments. Obviously, the fate of hyperosmotic active ions during dehydration avoidance involves a complex interplay of uptake, compartmentalisation and synthesis of compatible organic solutes. These processes collectively enable plants to maintain osmotic homeostasis and protect cellular integrity in the face of environmental stressors induced by abrupt deviation from the root-to-shoot ratio from the normal seasonal cycles.

7.2.1.4.6. Stomatal Regulation and Transpiration Management

Another critical component of dehydration avoidance is the regulation of stomatal conductance. Stomata play a dual role in maintaining hydration while allowing CO_2 exchange for photosynthesis. High Na^+ and Cl^- levels signal the guard cells to close the stomata, reducing transpiration loss [4]. Also, under water stress, abscisic acid increases in leaf tissues, promoting stomatal closure and thus

doi:10.20944/preprints202510.0892.v1

reducing water loss [53], which inherently limits CO_2 intake, leading to decreased photosynthesis and lower carbohydrate production [13]. Prolonged stomatal closure can lead to decreased fruit size and yield, a key concern in citriculture [38]. Others demonstrated that regulated deficit irrigation, where water stress is strategically induced, can enhance drought tolerance without severely impacting photosynthesis [59]. The outlined six critical intrinsic cellular activities, especially in responses to the repeated reduced root-to-shoot ratios at the demise of female nematodes, which induces root pruning-like effects, play a central role in the onset and progression of slow decline in citrus trees. The depletion of K^+ ions in the affected trees, the accumulation of Na^+ and Cl^- ions in leaf tissues, and the imbalances in hormones and sucrose partitioning, collectively impair root functions, reduce canopy density, and decrease fruit yield. Field observations have confirmed that citrus trees suffering from slow decline exhibit elevated Na^+ and Cl^- levels in leaf tissues, above the physiological toxicity thresholds of 0.10% for Na^+ and 0.25% for Cl^- ions [41]. Poor response to K fertilisation occurs unless *T. semipenetrans* population densities are reduced [52], suggesting that physiological imbalances cannot be corrected solely through nutrient supplementation.

8. Strategies for Managing Nematode-Induced Root-to-Shoot Ratio Reductions

Given the significant physiological consequences of repeatedly deviating the root-to-shoot ratios from its normal seasonal cycle, targeted management strategies are essential to maintaining citrus tree health, productivity and longevity. Three such strategies are being provided to illustrate the point.

8.1. Shoot Pruning Management

Light shoot pruning during winter dormancy, which increases the root-to-shoot ratio, can counteract the negative effects of root loss, thereby promoting a better balance in the ratio [32]. Additionally, avoiding excessive root pruning during mechanical weed management can prevent sudden, but disruptive peaks in sucrose transport and osmotic imbalances. Mowing between the rows and using herbicides within the dripline prevent root pruning. Evidence suggests that citrus roots from trees in adjacent rows may intermingle, which explained the spreading decline of citrus, induced by the burrowing nematode (*Radopholus citrophilus)* in Florida, USA [1].

8.2. Soil and Nutrient Management

Maintaining adequate K levels in the soil can help mitigate K^+ diffusion from roots into the rhizosphere and its subsequent downstream effects on starch metabolism. Soil amendments, such as organic amendments, active biochar and gypsum, can improve ion partitioning and reduce salinity stress [24].

8.3. Integrated Nematode Management

Managing *T. semipenetrans* populations through using integrated management systems that integrate nematode-resistant rootstocks, synthetic chemical nematicides, biocontrol agents such as *Trichoderma* species and/or the cucurbitacin phytonematicides can help to preserve the integrity of the root systems [25,59]. Reducing nematode-induced root pruning effects at female death after maturity can prevent the triggering of hydration avoidance that invariably leads to slow decline symptoms.

9. Fate of Hyperosmotic Active Ions During Dehydration Avoidance: A Detailed Analysis

Plants continuously experience environmental stressors that threaten their water balance and overall health. Among these stressors, salinity, drought and nematode infections impose significant osmotic challenges, forcing trees to implement drastic physiological and biochemical responses to maintain cellular homeostasis. In citrus trees, the phenomenon of slow decline, primarily induced by *T. semipenetrans* infections, is closely linked to dehydration avoidance caused by the deviation of the root-to-shoot ratio from its typical seasonal cycle. A critical aspect of this response is the redistribution and fate of hyperosmotic active ions, particularly K^+, Na^+ and Cl^-, which play key roles in dehydration avoidance mechanism [13,49]. Hyperosmotic active ions are essential for maintaining cell turgor, regulating water uptake, and preventing ion toxicity. However, in citrus trees affected by *T. semipenetrans*, the natural effects of root pruning occur at female death, leading to severe physiological consequences, including leaf chlorosis, fruit size reduction, sparse foliage, twig dieback and gradual tree decline [46]. This review explored the mechanisms through which hyperosmotic ions are regulated in citrus trees experiencing dehydration avoidance, emphasising ion movement, storage, and their ultimate impact on tree health. The abnormal mobilisation of hyperosmotic active ions due to reduced root-to-shoot ratios has serious implications for citrus orchard management. Promoting the root-to-shoot ratio to remain synchronised with its seasonal cycle is central to the management of slow decline of citrus. As outlined throughout this review, various strategies are available to prevent the deviation of the root-to-shoot ratio from its customary seasonal cycle. Additionally, maintaining adequate soil K^+ levels through balanced fertilisation programmes can help mitigate K^+ depletion, while regular leaching of soil with fresh water can prevent excessive salt accumulation and limit Na^+ and Cl^- ion toxicity [24]. Light shoot pruning can help compensate for root loss and stabilise ion distribution. Avoiding aggressive root pruning during mechanical weed management can minimise osmotic imbalances [32]. Managing *T. semipenetrans* populations through biocontrol agents or cucurbitacin-based phytonematicides, can reduce root pruning effects induced by female T. *semipenetrans* at death [25]. Rootstocks with both resistance to nematodes and tolerance to salinity, should be prioritised in citrus breeding programmes [3].

10. Conclusions

The slow decline of citrus is a complex syndrome driven primarily by *T. semipenetrans* infection, exacerbated by abiotic stress factors such as salinity and nutrient imbalances. The physiological mechanisms underlying this decline involve disruptions in the root-to-shoot ratio from the standard seasonal cycle, which trigger dehydration avoidance mechanism in root cells that eventually result in ion toxicity avoidance mechanisms in leaf cells. The imbalance consistently leads to excessive accumulation of Na^+ and Cl^- ions in leaves while depleting essential nutrients like K^+ in the entire tree, impairing photosynthesis and reducing fruit size and yield. Research has demonstrated that *T. semipenetrans* infection amplifies salinity-induced stress responses, altering the natural ion partitioning processes within citrus trees. The root pruning effects of female nematodes at death reduce root mass, which in turn disrupts osmotic balance and nutrient allocation. Dehydration avoidance compromises overall loss in tree vigour, leading to sparse foliage, small leaves, leaf chlorosis, twig dieback, fruit size reduction, and premature orchard health decline. This review highlights the importance of avoiding forcing the trees into dehydration avoidance processes through maintaining a natural optimal root-to-shoot ratio through integrated management strategies. Light shoot pruning during winter dormancy can help stabilise this balance, while aggressive root pruning during mechanical weed management during shoot flushes should be avoided to prevent exacerbating the slow decline of citrus. Additionally, soil fertility management, including the maintenance of adequate K^+ levels and management-led irrigation practices, play a crucial role in mitigating osmotic stress. Biological and chemical nematode management measures, such as cucurbitacin-based phytonematicides, organic amendments and nematophagous microorganisms, provide viable alternatives to synthetic chemical nematicides and should be integrated into citrus orchard management plans. Additionally, the selection of salt-tolerant and nematode-resistant rootstocks is essential for sustaining orchard productivity in saline environments. In conclusion, the slow decline of citrus is best managed through a holistic multipronged approach that includes ensuring that the cultural practices are intended to promote the synchronisation of the root-to-shoot ratio to the normal seasonal cycle, through *enter alia*, light shoot pruning strategies, soil and water management, and adequate management of *T. semipenetrans* population densities. Future research should explore the molecular pathways regulating root-to-shoot homeostasis and the potential for breeding rootstocks with enhanced tolerance to both biotic and abiotic stresses. By integrating the proposed strategies, citrus growers can improve tree longevity, sustain fruit production, and mitigate the adverse effects of slow decline, ensuring the long-term viability of citrus orchards.

Author Contributions: The authors contributed equally.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability: All data are available in the manuscript.

Acknowledgments: This work is based on the research supported in part by the Agricultural Research Council-National Department of Agriculture-University of Limpopo Centre for Excellence in Climate-smart Agriculture.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Duncan LW. Managing Nematodes in Citrus Orchards. In: Ciancio A, Mukerji KG, editors. Integrated Management of Fruit Crop Nematodes: Integrated Management of Fruit Crops and Forest Nematodes. Dordrecht: Springer Science (2009). p. 135-173.
2. Meena AK, Dutta F, Marak MC, Meena KK. Citrus decline. *Int J Curr Microbiol App Sci* (2018) **7**(4):2807-2815.
3. Verdejo-Lucas S, McKenry MV. Management of the citrus nematode, *Tylenchulus semipenetrans*. *J Nematol* (2004) 36(4):424-432.
4. Duncan LW, Noling JW. Modeling population dynamics of *Tylenchulus semipenetrans* on citrus grove. Proc Soil Crop Sci FL (1988) 47:250.
5. Syvertsen JP, Levy Y. Salinity interactions with other abiotic and biotic stresses in citrus. *HorTechnol* (2005). 5:100-103.
6. Labanauskas CK, Baines RC, Stolzy H. Effect of the citrus nematode *Tylenchulus semipenetrans* and two levels of water suction on nutrient concentration in navel orange leaves and roots. *Soil Sci* (1965) 99:367-374.
7. Hamid GA, Van Gundy SD, Lovatt CJ. Citrus nematode alters carbohydrate partitioning in Washington navel orange. *J Amer Soc Hort Sci* (1985) 110:642-646.
8. Krasniq AL, Blanke MM, Kunz A, Damerow L, Lakso AN, Meland M. Alternate bearing in fruit tree crops: past, present and future. *Acta Hortic* (2017) 1177:241-248.
9. Smith PF. Collapse of 'Murcott' Tangerine trees. *J Amer Soc Hort Sci* (1976) 101:23-25.
10. O'Bannon JH, Esser RP. Citrus declines caused by nematodes in Florida. II. Physiological races. (1985). Nematol. Cir. No. 116. Fla Dept Agric Cons Serv Div Pl Indus, Gainesville.
11. Shokoohi, E, Duncan LW. Nematode Parasites of Citrus. In: Luc M, Sikora RA, Bridge J, editors Nematode Plant Parasitic Nematodes in Subtropical and Tropical Agriculture. Wellington, UK: CABI (2018). p. 446-476.
12. Mashela PW, Nthangeni ME Interaction effects of citrus rootstocks, salinity and *Tylenchulus semipenetrans* parasitism on osmotically active ions. J *Phytopathol* (2002a) 150: 60-64.
13. Mashela PW, Nthangeni ME. Osmolyte allocation in response to *Tylenchulus semipenetrans* infection, root pruning and stem girdling. *J Nematol* (2002b) 34:273-277.
14. Syvertsen JP, Hanlon EA. Citrus trees stresses: Effects on growth and yield. (2008). Univ. of Florida-IFAS, Gainesville, FL, Publ. # HS1138.
15. Cohn E. Observations on the survival of free-living stages of the citrus nematode. Nematologica (1966) 12 :321-327.

16. Zhou W, Arcot Y, Medina RF, Bernal J, Cisneros-Zevallos L, Akbulut MES. Integrated Pest Management: An Update on the Sustainability Approach to Crop Protection. *ACS Omega* (2024) Se28;9(40):41130-41147. PMCID: PMC11465254.
17. Prasad SK, Chawla ML. Observations on the population fluctuations of citrus nematode, *Tylenchulus semipenetrans* Cobb, 1913. *Indian J Entomol* (1965) 27:450-454.
18. Salem AA. Observations on the population dynamics of the citrus nematode, *Tylenchulus semipenetrans* in Sharkia Governorate. *Egypt J Phytol* (1980) 12:31-34.
19. Vilardebo A. Study on *Tylenchulus semipenetrans* Cobb in Morocco. II. *Al Awamia* (1964) 11:31-49.
20. Ferris H.) Density-dependent nematode seasonal multiplication rates and overwinter survivorship: A critical point model. *J Nematol* (1985) 17:93-100.
21. Mashela PW, De Waele D, Dube Z, Khosa M C, Pofu KM, Tefu G, Daneel MS, Fourie H. In: Fourie H, Spaull VS, Jones RK, Daneel MS, De Waele D, editors. Alternative Nematode Management Strategies. Nematology in South Africa: A View from the 21st Century. Cham, Switzerland: Springer Nature (2017). p. 151-181.
22. Liu DL, An M, Johnson IR, Lovett JV. Mathematical modelling of allelopathy. III. A model for Curve-fitting Allelochemical Dose Response. *Nonlin Biol Toxicol Med* (2003). 1:37-50.
23. Machmer JH. Effect of soil salinity on nematodes in citrus and papaya plantings. *J Rio Grande Val Hort Soc* (1958)12:57-60.
24. Mashela PW, Duncan LW, Graham JH, McSorley R. Leaching soluble salts increases population densities of *Tylenchulus semipenetrans*. *J Nematol* (1992a) 24:103-108.
25. Mashela PW, Pofu K M. Influence of cucurbitacin-containing phytonematicides on selected nutrient elements in leaf tissues of green bean under greenhouse conditions. *Acta Agr Scand Section B – Soil & Pl Sci* (2017) *67*(8):743-747.
26. Rumiani M, Karegar A, Hamzehzarghani H. Population dynamics of the citrus nematode *Tylenchulus semipenetrans* Cobb, 1913 in an infested orchard in Fars province, southern Iran. (2023). R*es Square* doi: https://doi.org/10.21203/rs.3.rs-3585538/v1
27. Kumari S, Singh S. Study of fluctuations in the population of citrus nematode (*Tylenchulus semipenetrans*) in the North Bihar. *Int J Plant Pathol Microbiol* (2024) 4(1):8-10.
28. Martínez-Vilalta J, Sala A, Asensio D, Galiano L, Hoch G, Palacio S, Piper IF, Lloret F. Dynamics of non-structural carbohydrates in terrestrial plants: a global synthesis. *Ecol Monograph* (2016) 86 (4):495-516.
29. Budiarto R. Poerwanto R, Santosa E, Efendi D. A review of root pruning to regulate citrus growth. *J Trop Crop Sci* (2019) 6(01):1-7. 8-10.
30. Duncan LW, Graham JH, Timmer LW. Seasonal patterns associated with *Tylenchulus semipenetrans* and *Phytophthora parasitica* in the citrus rhizosphere. *Phytopathol* (1993) 83:573-581.
31. Mashela P W. Undefeatable Enemies: Answering Questions with Questions. Sovenga, South Africa: University of Limpopo Press (2007). p. 38.
32. Eissenstat DM, Duncan LW. Root growth and carbohydrate responses in bearing citrus trees following partial canopy removal. *Tree Physiol* (1992)10:245-257.
33. Bohn HL, McNeal BL, O'Connor GA. (1985). Soil Chemistry. New York: Wiley.
34. Mass EV. Salinity and citriculture. *Tree Physio*l (1993) 12:195-216.
35. Dropkin VH, Martin GC, Johnson RW. Effect of osmotic concentration on hatching of some plant-parasitic nematodes. *Nematologica* (1958) 3: 115-126.
36. Kirkpatrick JC, Van Gundy SD. Soil salinity and citrus nematode survival. *Nematologica* (1966) 12: 93-94.
37. Viglierchio DR, Croll NA, Gortz JH. The physiological response of nematodes to osmotic stress and an osmotic treatment for separating nematodes. *Nematologica* (1969) 15:15-21.
38. Duncan LW, Mashela PW, Fergurson J, Graham J, Abou-Setta MM. and El-Morshedy MM. Estimating crop loss in orchards with patches of mature citrus trees infected by *Tylenchulus semipenetrans*. *Nematropica* (1995) 25: 43-51.
39. O'Bannon JH, Esser RP. Citrus declines caused by nematodes in Florida. II. Physiological races. (1985) Nematol. Cir. No. 116. Fla Dept Agric Cons Serv Div Pl Indus, Gainesville.
40. McSorley R. Adaptations of nematodes to environmental extremes. *FL Entomologist* (2003) 86(2) :138-142.

41. Syvertsen JP, Lloyd J, Kriedemann PE. Salinity and drought stress effects on foliar ion concentrations, water relations and photosynthetic characteristics of citrus orchards. *Austral J Agric Res* (1988) 39:619-627.
42. Duncan RP, Dexter N, Wayne A, Hone J. Eruptive dynamics are common in managed mammal populations. *Ecology* (2020)101(12):e03175. 10.1002/ecy.3175
43. Mashela PW, Duncan LW, Graham JH, McSorley R. Leaching soluble salts increases population densities of *Tylenchulus semipenetrans. J Nematol* (1992a) 24:103-108.
44. Duncan LW, Graham JH, Timmer LW. Seasonal patterns associated with *Tylenchulus semipenetrans* and *Phytophthora parasitica* in the citrus rhizosphere. *Phytopathol* (1993) 83:573-581.
45. Duncan LW (2009) Managing Nematodes in Citrus Orchards. In: Ciancio A, Mukerji K, editors. Integrated Management of Fruit Crops Nematodes: Integrated Management of Plant Pests and Diseases, vol 4. Dordrecht: Springer. p. 135-173.
46. Mashela PW. Interactions of *Tylenchulus semipenetrans* infection, soil salinity and citrus rootstocks. PhD dissertation. Gainesville, University of Florida. (1992).
47. Cooper WC. Toxicity and accumulation of salts in citrus trees on various rootstocks in Texas. *Proc. Fla. State Hort Soc* (1961)74:95-104.
48. Mashela PW, Duncan LW, McSorley R. Salinity reduces resistance to *Tylenchulus semipenetrans* in citrus rootstocks. *Nematropica* (1992b) 2:7-12.
49. Waisel Y. Biology of Halophytes. New York: Academic Press (2012). p. 410.
50. Verdejo-Lucas S, McKenry MV. Management of the citrus nematode, *Tylenchulus semipenetrans*. *J Nematol* (2004) 36(4):424-432.
51. Levy Y, Syvertsen P. Irrigation water quality and salinity effects in citrus trees. *Hort Rev* (2004) 30: 37-82.
52. Fouche PS, Bester DH, Veldman GH. The influences of potassium applications and nematicides on the potassium nutrition of Valencia orange trees on replant citrus soils. *J Amer Hort Sci* (1977) 102:546-547.
53. Ford BJ. Physiology of Woody Plants. San Diego: Academic Press. (2007). p. 318.
54. Epstein E. Mineral Nutrition of Plants: Principles and Perspectives. New York: Wiley. (1972). p. 412.
55. Harding RB, Chapman HD. Progress report on a study of soil characteristics in forty high-performance orange orchards in California. *Soil Sci Soc Amer Proc* (1951) 15:243-248.
56. Salisbury FB, Ross C W. Plant Physiology. Wadsworth: Belmont. (1992). p. 682.
57. Matias P, Barrote I, Azinheira G, Continella A, Duarte A. Citrus pruning in the Mediterranean climate: A review. *Plants* 12:3360. Doi. Org/10.3390/plants121933
58. Moya JL, Gomez-Cadenas, A, Primo-Millo E, Talon M. Chloride absorption in relative salt sensitive Carrizo citrange and in salt tolerant Cleopatra mandarin citrus rootstocks is linked to water use. *J Exp Bot* (2003) 54 : 8825-8833.
59. Guzmán-Guzmán, P, Etesami H, Santoyo G. *Trichoderma:* a multifunctional agent in plant health and microbiome interactions. *BMC Microbiol* (2025) 25:434 (2025) doi.org/10.1186/s12866-025-04158-2