agronomy

Review

Recent Achievements and New Research Opportunities for Optimizing Macronutrient Availability, Acquisition, and Distribution for Perennial Fruit Crops

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Abstract: Tree responses to fertilizer management are complex and are influenced by the interactions between the environment, other organisms, and the combined genetics of composite trees. Increased consumer awareness of the environmental impact of agriculture has stimulated research toward increasing nutrient-use efficiency, improving environmental sustainability, and maximizing quality. Here, we highlight recent advancements and identify knowledge gaps in nutrient dynamics across the soil–rhizosphere–tree continuum for fruit crops. Beneficial soil management practices can enhance nutrient uptake and there has been significant progress in the understanding of how roots, microorganisms, and soil interact to enhance nutrient acquisition in the rhizosphere. Characterizing root architecture, in situ, still remains one of the greatest research challenges in perennial fruit research. However, the last decade has advanced the characterization of root nutrient uptake and transport in plants but studies in tree fruit crops have been limited. Calcium, and its balance relative to other macronutrients, has been a primary focus for mineral nutrient research because of its important contributions to the development of physiological disorders. However, annual elemental redistribution makes these interactions complex. The development of new approaches for measuring nutrient movement in soil and plant systems will be critical for achieving sustainable production of high-quality fruit in the future.

Keywords: soil–plant interactions; rootstock; soil fertility; rhizosphere; soil ecology; orchards

1. Introduction

In perennial fruit crops, effective nutrient management is required to carefully control nutrient supply and maintain balanced tree nutrition to maximize resource-use efficiency and optimize crop yield, fruit quality, and nutritional value. Given that nutrient deficiencies can influence production over multiple growing seasons, significant effort has been focused on better understanding the factors controlling nitrogen (N), phosphorus (P), calcium (Ca), magnesium (Mg), potassium (K) and sulfur (S) dynamics in orchard systems. That being said, nutrient imbalances frequently arise due to synergistic or antagonistic interactions at the rhizosphere and/or whole-plant level [1]. These relationships can have an impact on disorder incidence and overall fruit quality causing economic losses for producers. Effective amelioration of mineral nutrient imbalances can depend on several interacting edaphic factors, including climate, soil properties, crop, rootstock and scion cultivar, and historical management practices. In commercial orchards, for example, fertilization is normally recommended when deficiencies are identified through soil testing and/or at the onset of symptoms in leaves or fruit. Perennial fruit crop management must limit over-fertilization that can reduce profitability and cause environmental harm. Furthermore, careful nutrient management can reduce the incidence of physiological disorders and enhance postharvest quality and storability. A comprehensive understanding of the movement and availability of mineral nutrients within the rhizosphere, the dynamics of nutrient uptake by roots and symbiotic organisms, and the subsequent partitioning of mineral nutrients within the scion are important for advancing the development of effective practices for perennial-fruit-nutrition management.

One of the underlying goals of mineral nutrition research on perennial fruit trees is to enhance root acquisition of nutrients via the promotion of root development. Roots represent the primary pathway of nutrient movement from the soil to developing leaves, stems, and fruit. Studies beginning almost a hundred years ago [2] described the basic morphology of root systems of perennial fruit trees and how root architecture can change in response to the soil environment and vary among rootstock genotypes. Later, the periodicity of new-root growth and factors that impact this phenomenon were characterized [3]. In the past two decades, both of these approaches formed the field of functional root biology and identified the effect of horticultural practices, such as increased planting density, on root biology and nutrient dynamics [4]. However, the direct relationships between root architecture and periodicity and plant productivity still remains poorly understood.

The principal aims of mineral nutrition research on perennial fruit trees have been to optimize orchard nutrition, productivity, and quality. These include improving mineral nutrient acquisition through agronomical practices of fertilization and/or enhancing root acquisition of nutrients via the promotion of root development. A clear and comprehensive understanding of the movement and availability of mineral nutrients in the soil, interactions between nutrients within the rhizosphere, dynamics of nutrient uptake by roots and mycorrhizae, and partitioning of scion mineral nutrients between vegetative growth and developing fruit are important for advancing the development of effective practices for perennial-fruit-nutrition management (Figure 1). Although mineral nutrient issues are not limited to macronutrient management, recent reviews have addressed micronutrients in perennial fruit crops [5,6]. Here, we review recent scientific advances in our understanding of macronutrient nutrition and identify gaps and opportunities for improving sustainable nutrient management in perennial fruit crops. This review aims to update the information provided in comprehensive earlier reviews [7–9], which formed the foundation for the scientific advances described below.

2. Mineral Nutrient Cycling in Perennial Fruit Crops

Nutrient reallocation in perennial tree fruit can occur within a single year (e.g., translocation from senescent leaves to fruits or to younger leaves) and between years. The latter process is a strategy used by deciduous trees to uncouple vegetative growth from root nutrient uptake and to retain absorbed nutrients during leaf senescence. These nutrients can then be remobilized to support fruit and vegetative growth shortly after budbreak. Nutrient remobilization and retention from senescing leaves depend on nutrient mobility within the phloem and on seasonal patterns of leaf senescence. For example, calcium (Ca) is almost entirely lost via leaf abscission, while N, P, and K are largely remobilized back into stems and roots prior to leaf senescence. The amount of nutrients involved in such fluxes depends on tree size and nutrient status [10]. Figure 1 depicts the major pathways of macronutrient movement into, out of, and within (i.e., reallocation) fruit trees. Absorbed nutrients (n. 1 in Figure 1) that are allocated to fruits are removed from the orchard at harvest (n.2 in Figure 1), while those partitioned to shoots and leaves can be translocated within the tree (n.3 in Figure 1), or are transferred to the soil via abscised leaves and pruning wood (n.4 in Figure 1), where they can become available for uptake again. These responses are complex and difficult to quantify because pre-existing nutrient pools are often large and dynamic.

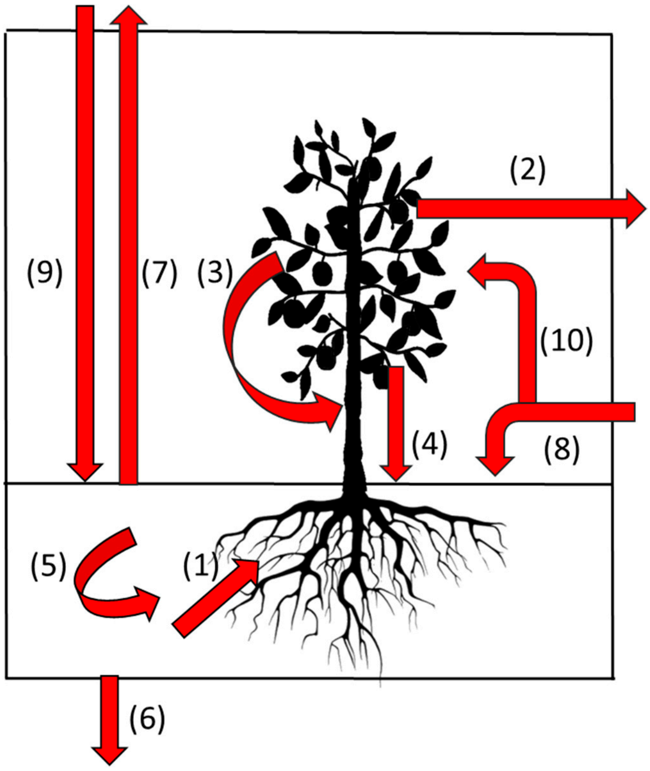

Figure 1. Schematic diagram of nutrient fluxes in orchard systems. (1) Nutrient uptake, (2) Nutrient export with harvested fruits, (3) Internal nutrient cycling; (4) Nutrient transfer to the soil by abscised leaves and pruning wood, (5) Organic matter decomposition and nutrient cycling in the soil, (6) nutrient leaching and erosion, (7) Emissions of nutrients in a gaseous form, (8) fertilizer nutrients, (9) nutrient deposition (including nutrients in the irrigation water), and (10) foliar fertilizer applications.

Nutrient reallocation between seasons requires mineral nutrient withdrawal from senescent leaves in autumn, storage over winter, and remobilization in spring. Most of the existing knowledge about these processes has been derived from N flux measurements using the stable isotope, ^{15}N. During the growing season, the leaf transitions from a carbon source to a source of mineral nutrients that are stored during the dormant period [11]. The proportion of N withdrawn during leaf senescence can range from 20% to 80% [12] of the total leaf N and represents a significant N source for developing flowers and vegetative growth the following spring. This can equal 30 kg N ha^{-1} $year^{-1}$ in peach trees [13]. For more dwarfing fruit trees, like those used in modern apple orchards, these pools are substantially smaller. Leaf N withdrawal in autumn only accounts for a portion of remobilized N the following spring for apple [14]. Remobilization in spring provides N to support the early stages of leaf, flower and fruitlet metabolism, until root uptake becomes the predominant source of N. The duration of the remobilization period in spring affects the optimal timing of N fertilizer applications. Although remobilization is not affected by the amount of soil N available for uptake in spring, the duration of remobilization can increase (up to 60 days from bud burst) if trees have larger pools of stored N [15]. While N remobilization has been clearly described, the measurement of remobilization for other macronutrients has been limited to date. With the development of new approaches to measure changes in nutrient fluxes across plant tissues and into the soil environment, it is now more feasible to measure within-tree fluxes for all macronutrients.

Abscised leaves, pruning wood, and mowed material derived from herbaceous plants growing between tree rows (n.3 in Figure 1) contain significant amounts of nutrients [11]. Pruned wood and fallen leaves account for the largest N removal from grapes [16] and incorporation into the soil within rows could represent a significant addition of N to the system. During their decomposition, these sources can provide a significant portion of macronutrients available for uptake [17]. K release during leaf decomposition occurs rapidly. Approximately 70–80% of the K from abscised leaves is already available in the soil underneath the litter in the following spring. N release is less rapid and is mostly complete within three years after leaf abscission [18]. Pruning wood normally has a higher C/N ratio and contains lower nutrient concentrations than abscised leaves. Regardless of whether this woody material remains on the soil surface or is incorporated into the soil, it typically decomposes more slowly than herbaceous material and nutrient release rates are not easy to estimate (n.5 in Figure 1). It is clear that nutrient cycling within perennial fruit crops must consider dynamic soil processes and aboveground management practices since both affect the availability of nutrients for plant uptake.

3. Soil Nutrient Cycling

Mineral nutrients are transported in the soil toward roots through a variety of mechanisms. They are generally grouped as follows: highly mobile nutrients, such as N are carried in soil solution via mass flow; P and K diffuse via the films of water surrounding soil particles; P is also taken up directly via root interception of soil particles; other nutrients, such as Ca, Mg, and S are transported via some combination of these processes. Nutrient mobility via mass flow and diffusion is markedly dependent on both soil moisture content and soil hydraulic conductivity. Management practices aimed at improving water- and nutrient-use efficiency, such as the increased use of organic amendments and cover crops (described above), efficient water management via irrigation scheduling, and fertigation all have the potential to alter soil nutrient dynamics in perennial fruit systems (Figure 2A).

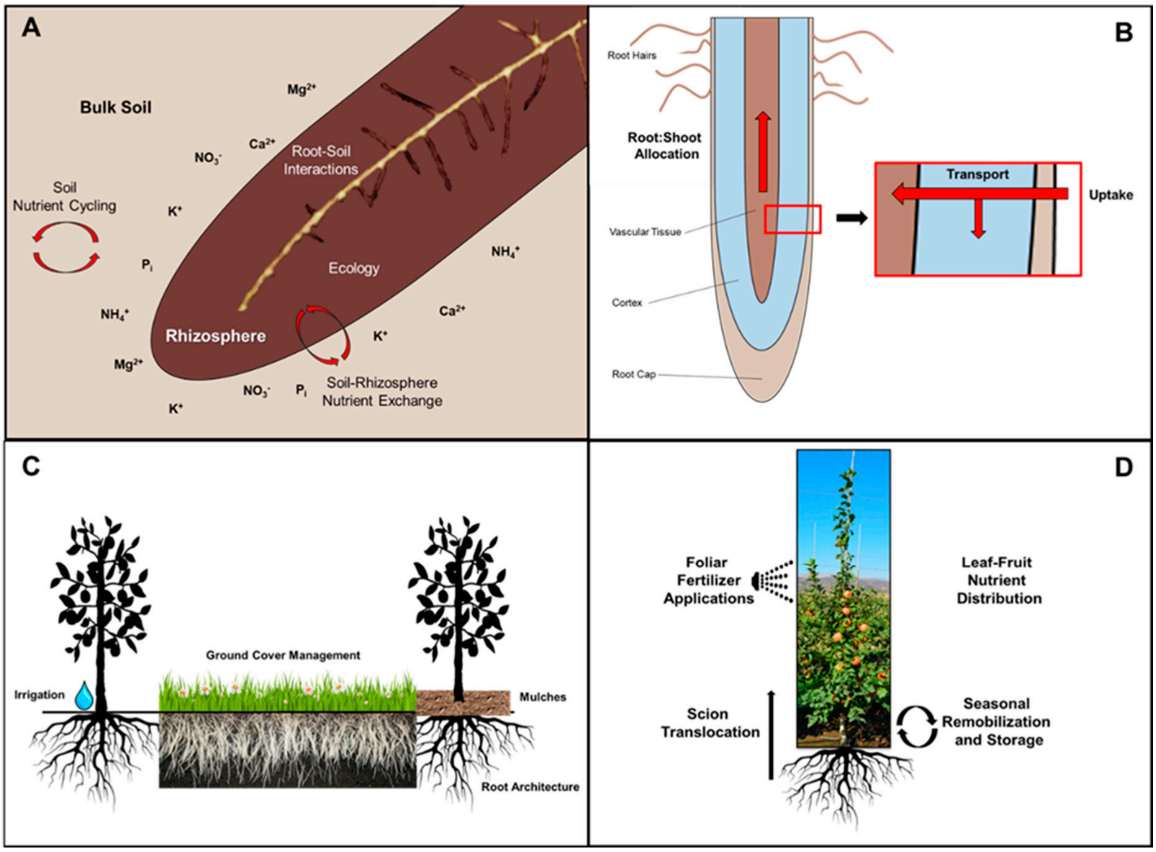

Figure 2. Soil and rhizosphere (**A**), root (**B**), orchard (**C**), and above-ground (**D**) factors affecting nutrient composition of perennial fruit crops.

4. Soil Carbon

Soil carbon and organic matter management can have long-lasting impacts on orchard productivity. Inter-row cover cropping, retention of on-farm sources of organic matter (e.g., prunings), and application of off-farm sources of organic matter (e.g., composts and organic mulches) all can potentially increase soil organic carbon (SOC) stocks in perennial fruit cropping systems [19,20]. For example, amendments with olive mill waste have been reported to improve carbon sequestration in soils and improved N, P, and K availability in olive groves [21]. The use of fescue (*Festuca arundinacea* Schreb) has been reported to increase soil organic carbon and microbial biomass C in grapes [22]. Amendments or cover crops have the potential to increase soil organic carbon and stimulate soil microbial activity in perennial fruit cropping systems. The need to improve or, at least, maintain current soil organic matter has long been considered a tenet of sustainable orchard production, but has also recently received attention in conventional orchard management [23]. In olive, carbon budgeting has been used to measure soil carbon pools and storage [24]. Their practices are important to account for carbon sequestration occurring in orchards or for measure changes in soil organic carbon in response to changes in practices. Elevated levels of SOC have been reported to improve orchard replant success [25], particularly in cases where nutritional deficiencies exist [26]. Management practices that enhance organic matter content in orchard soils may reduce N-fertilizer losses via leaching or volatilization, and promote nutrient cycling [27–29]. Enhancing SOC stocks in agricultural soils as a means of mitigating atmospheric greenhouse gas emissions has also received considerable attention, although most of this work focused on field crops [30–32].

5. Soil Fertility

5.1. Nitrogen (N)

N management decisions for perennial fruit production systems are typically informed by soil N assays. However, quantifying N availability via soil analyses can be challenging because of high temporal, chemical, and spatial heterogeneity. Spatial variation in nutrient deficiencies must be carefully considered when collecting soil samples and when evaluating tree performance and productivity. N additions from organic sources like decaying leaves, clippings, grasses, rhizosphere N fixation, and/or N losses via leaching (Figure 1, no. 6) or denitrification (Figure 1, no. 7) make accurate measurements of available soil N difficult. More accurate and precise methods for estimating the timing and magnitude of N inputs from decomposing organic materials are needed to best inform N management as organic soil amendments are more frequently used [33].

Traditionally, N additions (n. 8 in Figure 1) were made through the addition of granular N or organic fertilizer inputs. Furthermore, atmospheric N deposition (n. 9 in Figure 1) has been reported as a significant source of N for trees, especially in areas with high population densities [34]. N requirements are increasingly being met via fertigation in both conventional and organic systems. N delivery using fertigation is being rapidly adopted because of the benefits of the direct delivery of fertilizer to the root system immediately surrounding the emitters through the application of water-soluble N forms directly to the soil. Given the increasing movement towards fertigation and since many mineral forms of N are readily soluble in soil solution, the measurement of NO_3-N and NH_4-N concentrations in soil are important for identifying site-specific interactions between irrigation practices and soil N availability [35]. N fertilizer applications can have an impact on soil qualities. For example, soil acidification can occur from long-term applications of ammonium-based N fertilizer, including in drip-irrigated orchards on coarse-textured soils with low buffering capacities. However, this issue can be simply mitigated by using non-acidifying N fertilizers, such as calcium nitrate for fertigation [36]. Increased adoption has brought a wider range of N-based fertilizers that are suitable across a range of soil conditions.

Nutrient loss is a critical factor affecting soil N dynamics that has been well described in annual field cropping systems, but not as much in perennial crop soils. N leaching and denitrification can compromise the efficiency of periodic N fertilization in fruit cropping systems. N emissions (n. 7 in Figure 1) are important fluxes for N cycling in perennial systems, while subsurface leaching (n.6 in Figure 1) is particularly important for NO_3-N forms whether derived from mineral or organic fertilizers. Precise irrigation practices can considerably limit N leaching through the soil profile. This is particularly true in coarse-textured orchard soils, where multiple daily applications of smaller volumes of fertigation are required to prevent leaching. Moreover, N leaching depends often on (i) the amount of residual mineral N below the root zone, (ii) the soil and (iii), the amount of water leaching. For instance, [37] report a large temporal variation of soil NO_3^- concentrations below the root zone (from < 1 mg L^{-1} to more than 2400 and 11,000 mg L^{-1} in almond and pistachio, respectively) when N supply ranged from 201 to 324 kg N ha^{-1} y^{-1} and N-leaching (averaged across some management techniques) was 92 kg N ha^{-1} y^{-1}. In an apple orchard, [38] estimated N leaching to be 18 to 22% of applied N (60 kg N ha^{-1} y^{-1}) and was dependent on orchard floor management.

N emissions from volatilization represent the other major source of N loss in perennial fruit systems. Gaseous emissions of N are greenhouse gases that can contribute to climate change [39]. Policy goals that limit emissions of potent greenhouse gases like N_2O have also stimulated interest in quantifying gaseous N_2O losses from a wider range of crops, soil types and geographic regions to better account for these losses for greenhouse gas accounting exercises. This should include perennial fruit cropping systems. For example, [27] reported that changes in irrigation frequency and applications of C-rich surface mulches suppressed the production of N_2O in a fertigated apple orchard in British Columbia, Canada. Additionally, [40] estimated that N_2O emissions from soil in an almond orchard subjected to fertigation by drip or microsprinkler systems were in the range of 0.6 to 1.6 kg N_2O-N ha^{-1}

y^{-1}. Surprisingly, emissions were significantly correlated with soil water-filled pore space and not with soil mineral-N. These results clearly indicate that agronomic practices can contribute to N_2O emissions and highlights the need for a more in-depth study of this phenomenon in the future. To adequately assess the impact of current fertilizer management practices on N emissions, more research is needed across a wider range of species, production systems, and geographic regions in the future.

5.2. Phosphorus (P)

Traditional soil testing to measure extractable soil phosphorus (P) has been traditionally difficult to associate with tree responses to P-fertilization [41]. In some soils, the formation of insoluble aluminum and iron phosphates at low soil pH and calcium phosphates at high soil pH can cause a significant limitation in the P mobility and, therefore, in the levels of P availability for plants in many soils. Better methods for estimating plant-available P from soil components (mineral particles and decaying organic matter) are needed to develop more appropriate P management strategies that improve perennial fruit growth and productivity. Fertigation has shown promise in increasing P availability in soils. For example, [36] reported that P fertigation can increase P mobility in soil compared to broadcast applications, especially in sandy soils. Often, organic amendments that are applied to orchard soils to increase soil N availability can also enhance available soil P pools [42]. Cover crops may also affect P availability in the orchard. For example, in table grape, the use of *Trifolium repens* L. as an inter-row cover crop increased P concentrations in leaves and fruit clusters [43]. Additionally, the use of surface mulches and composts in fertigated orchards and vineyards also promotes soil P cycling and improve P availability and is thought to be a consequence of increased soil phosphatase enzyme activity [44] and higher concentrations of ion-exchange resin P [28]. However, increased leaching of P below the root zone following compost application in an apple orchard suggests that compost applications may, in some cases, increase the risk of P-contamination of nearby water sources [45]. That being said, some organic amendments (e.g., shredded paper mulch) have been reported to promote P immobilization [46]. Therefore, organic inputs need to be characterized and considered individually for their contribution to soil P supply and availability to better inform organic production practices that can be variable in their supply of macronutrients including P. Similar to N, above-ground management practices have strong implications for P cycling and availability for uptake in orchard soils. The further development of strategies that improve P availability and uptake in orchards will improve precision fertilization approaches for P in perennial fruit production.

5.3. Potassium (K), Calcium (Ca), Magnesium (Mg), and Sulfur (S)

Similar to soil-based measurements for N and P, traditional soil test values for K, Ca, Mg, and S are also poor indicators of availability and uptake of these nutrients [47]. Like P, despite the importance of fruit Ca concentration to the quality of many fruits, there is generally a poor association between fruit and soil Ca levels [48]. Thus, soil Ca availability generally appears not to affect fruit Ca accumulation, even when soil pH is maintained by lime applications. However, high values of exchangeable (K + Mg)/Ca ratio in soils may increase the incidence of Ca-related fruit disorders, such as bitter pit. However, these results are difficult to replicate at the field level, even when K is applied through fertigation [49]. K availability can strongly vary within the orchard, including within and between rows, because of its high mobility. For example, low levels of extractable soil K and K-deficient symptoms were observed in the tree-row near the drip emitters even when there was no evidence for low K availability elsewhere in the orchard. High mobility of K in soils increases the risk of leaching of K from areas where high amounts of irrigation occur but, to date, few environmental impacts have been measured. Broadcast or water-soluble applications of K have been effective at quickly ameliorating K deficiencies. To maintain adequate available K in the root zone, annual K-fertigation is recommended for coarse-textured soils [36]. Organic amendments and cover crops can be effective in supplying base cations (particularly K) to orchards but need to be more objectively studied [50].

In orchards, S-deficiencies are rare and there is little information concerning crop response to S applications. The adoption of soil testing methods to determine soil S status and to guide S-fertilization recommendations has been limited [51]. Inadequate S is most likely to occur in highly leached soils with low organic matter content when there are few other applications of S in the course of production. Like other mineral nutrients, cover crops have been reported to increase S concentrations in both leaves and fruit [43]. These conditions do exist in some irrigated fruit-growing regions and the industry would benefit from clearer guidance on S fertilization in perennial fruit crops.

5.4. Effects of Organic Soil Amendments on Soil Nutrient Dynamics

Soil amendments like manures, composts, surface mulches, cover crops, and biochar can affect the size distribution and stability of soil aggregates [52]. In turn, these changes will affect soil porosity, soil pore size distribution and bulk density and cause consequent changes in soil hydraulic properties [53,54] that are inextricably linked to nutrient retention and availability in soils. Although increasing soil organic matter is often suggested as a strategy to improve soil moisture retention in the root zone, reported results have been mixed. A recent meta-analysis from over 60 studies across a range of agricultural systems concluded that a 1% increase in soil organic C improved available water capacity by only 1.17 mm 100 mm^{-1} [55]. Soil amendment-related improvements in soil water retention were greater at lower soil water potentials (i.e., saturation and field capacity (−10 kPa or −33 kPa, respectively), in coarse-textured soils, and in deeper soils (>30 cm). These findings suggest that applications of organic soil amendments may be particularly effective at improving soil water retention in orchard systems, which are often planted on coarse-textured soils, and for more deeply rooted tree fruit species and rootstocks.

Several recent studies have investigated the effects of soil organic matter (SOM) amendments on soil physical properties in perennial horticultural systems. For example, increased SOM content and aggregate stability and decreased soil bulk density were observed after four years of cover cropping with white clover in wine grapes [56] and after seven years of surface applications of alfalfa hay or bark mulch [44] in irrigated apples. Similar findings were reported after six years of mulch and compost applications in a heavily eroded apple orchard [57] and after only two years of leguminous cover-cropping in an apricot orchard [58]. Amendment-driven changes in soil physical properties can increase soil water content (θ) and change the soil moisture potential (ψ) and characteristic curve (θ vs. ψ) of orchard soils. For example, soil moisture contents were increased between saturation and 100 kPa in response to fall-applied composted dairy solids in a sandy almond orchard soil [59] and over the growing season in response to applications of compost and spray-on paper mulch in an apple orchard [60].

Organic soil amendments have the potential to improve soil moisture retention in some orchard systems. Cover crops are also useful in improving soil moisture retention in orchard systems [61]. It is possible that these cover crops can compete against limited water resources and care must be taken to select the correct cover crop for the correct environment. The use of surface mulches could also reduce the infiltration rate of applied irrigation water, thereby reducing soil moisture levels through the growing season. This issue may be more concerning when irrigation water is spread across the soil surface (e.g., via micro-sprinklers) than when it is concentrated over a small surface area (e.g., drip irrigation) [62]. However, another study identified the opposite where soil infiltration capacity increased with the addition of surface-applied organic composts in a drip-irrigated peach orchard [63]. These contradictory results suggest that the effect of surface mulches on soil properties need to be more fully explored to identify long-term changes to the orchard soil environment.

An increase in agronomic studies on the use of organic amendments on soil properties and fertility, mechanistic studies understanding the physical, chemical, and biological effects of these practices are needed. To improve research outcomes, new technologies are improving our ability to understand the mechanisms by which organic amendments interact with SOM, soil biota and soil minerals to influence soil water and nutrient dynamics. These include X-ray computed tomography

(CT) scanning, to determine how organic amendments alter the number, morphology and location of macro- and micro-pores and how these changes affect chemical transport through the soil [47], as well as ^{13} C-nuclear magnetic resonance (NMR) spectroscopy, to examine the role of organic matter chemistry in soil aggregate formation and hydrophobicity [64]. Furthermore, the growing research area of soil microbiomics can be used to evaluate amendment-caused changes in microbial physiology and diversity and how these changes influence soil C dynamics [65] and ultimately orchard growth and productivity [22]. A clear example of how amendments change soil enzyme activities, soil microbiological community structure, chemical composition, and soil fertility has been described using olive mill waste [66–69]. There are opportunities for coordinated studies across multiple species or amendments that may identify common patterns in changes that can be used to improve soil carbon sequestration and the subsequent benefits from these improvements.

5.5. Effects of Irrigation Management on Soil Nutrient Dynamics

Orchard irrigation management can be used to adjust nutrient supplies to roots in a number of ways: (i) by maintaining soil moisture content at optimum levels for transport through the soil (ii) by ensuring that water and nutrients are retained in the root zone and (iii), by adjusting the irrigation regime to the method of nutrient application (e.g., broadcast fertilizer, fertigation, organic amendments) to optimize nutrient availability [70]. Maintaining optimum soil moisture content and retaining water and nutrients in the root zone of temperate tree fruits can be achieved by scheduling irrigation to meet evapotranspiration (ET) requirements using micro-irrigation and deficit irrigation practices, as summarized in [70].

Nutrient analysis of the soil solution has been used to demonstrate that micro-irrigation can be effective at increasing N retention in the root zone compared with low-pressure sprinklers, particularly if N is supplied via high-frequency, low-volume fertigation [70]. In contrast, large single doses of P in conjunction with micro-irrigation can increase P in the soil solution over a longer period compared with the application of multiple doses, likely by saturating soil P adsorption sites. [28] used ion-exchange resins to measure NO_3-N in the soil and reported that concentrations were higher under drip irrigation than under micro-sprinkler irrigation. Surface mulches work to limit water losses through evaporation but also affect nutrient cycling and movement in the soil. Surface mulches can work to immobilize N, reducing available soil NO_3-N [28]. By contrast, in another study, applications of compost increased ortho-PO_4 availability, particularly when compost was applied in combination with mulch. However, the irrigation method had no effect.

The effects of soil and water management on nutrient movement in the soil can be directly measured from the analysis of soil leachates which assess the movement of nutrients out of the root zone through the mass flow of water. Leaching of both N and P below the rooting zone of a high-density fertigated apple planting (Figure 1, no.5) has been attributed to the over-application of irrigation water, despite irrigation scheduling based on ET-replacement [45]. In this study, however, more N was lost to leaching in high N treatments and, in one of the three study years, to compost additions. In contrast, ortho-PO_4 leaching was accelerated by increased application of compost. Similarly, leaching losses of N in the form of NO_3^- were accelerated by over-watering, high concentrations of N in the irrigation water, and repeated applications of poultry manure [29]. Clearly, careful manipulation of water and nutrient application rates and timing are required to effectively retain nutrients within the rooting zone, thereby protecting water quality, promoting efficient fertilizer use, and maintaining healthy tree nutrient status. These must be counterbalanced by the effect of other minerals in the irrigation water such as sodium that can have negative consequences on plant growth. The need for increased precision in the temporal and spatial application of water and nutrients to orchard crops is driving recent trends in research [70] (Figure 2B). These include (i) improved techniques for sensing water and nutrient deficits at the plant and landscape scale, (ii) automation of irrigation and nutrient management at the individual tree and orchard scales, and (iii) improved understanding of cultivar and rootstock influences on water and nutrient use through genomics [29].

6. Nutrient Interactions in the Rhizosphere

In perennial agroecosystems, the rhizosphere is the most active soil region involved in plant nutrient-acquisition and is the main soil zone for microorganism-affected nutrient cycling, C sequestration, and soil organic matter processes [71]. It is a soil zone with concentrated complex chemical, biological, and physical interactions shaped by the interplay between roots, microorganisms, and soil [72]. In this unique soil volume, nutrient availability and mobilization, as well as the rates of mineral nutrient uptake are affected by various factors which can include: (i) climatic conditions; (ii) soil type; (iii) plant species and genotypes; (iv) plant nutritional states; (v) agronomic practices; (vi) root-associated microbiome and (vii) the dynamic interaction among all those factors [73,74].

A broad spectrum of low and high molecular weight organic compounds such as organic acids, sugars, amino acids, and phenolic compounds are synthesized by plant tissues and then exuded into the rhizosphere by roots [75]. Indeed, up to 30% of the C reaching the roots is released into the rhizosphere as root exudates [76,77]. Once in the rhizosphere, these compounds significantly contribute to the soil organic C pool and the agroecosystem C cycle. Exudates can affect the chemical and physical soil composition directly influencing its pH and/or its exudate-driven metal-complexing properties [78] consequently enhancing the availability of nutrients such as P. When the mineral nutrient availability is close to thresholds for deficiency or toxicity, synergisms and/or antagonisms within the rhizosphere that either enhance or suppress availability are even more important. In fact, unbalanced nutrient availability at the soil–root interface can influence whole plant nutrient demand since it affects the growth, the uptake, allocation, and assimilation rates of other nutrients [79].

Plant exudates in the rhizosphere also foster a diverse ecosystem of microorganisms. In one gram of agricultural soil, the number of bacterial cells ranges between 10^9 to 10^{10}, and in the rhizosphere, the density can increase up to 10^{13} [80]. Some of these microbes, which naturally occur in the rhizosphere, may mobilize a wide range of nutrients and enhance plant mineral acquisition [78,79] and plant health in marginal soils. Plant exudates in the rhizosphere are important avenues for communication between microbes and plants. For example, the chemotactical attraction of fungal and bacterial species from the surrounding bulk soil towards the roots can promote vegetative growth [81–83]. Moreover, some of these microbes can sometimes act as growth-promoting rhizobacteria (PGPR) and plant growth-promoting fungi (PGPF) [84]. These two groups (PGPR and PGPF) are not associated with a specific taxonomic group, but they are characterized by huge phylogenetic heterogeneity [79]. Specifically, microbes in the rhizosphere have been extensively demonstrated to solubilize P from phosphate minerals, transform mineral N into organic forms [85]. While there have been clear examples of how specific microbial species or groups can affect nutrient availability, there is a general lack of knowledge about the multilevel community organization and the inter-kingdom associations (i.e., Fungi and Bacteria) and the role that these communities/associations can play in plant nutrient acquisition. It is well known that fungi and bacteria often share the same ecological niches where co-occurrences can result in mutual interactions [86]. These inter-kingdom relationships can then promote the co-evolution of specific communities crucial in agricultural soil for plant and/or fruit development [87,88]. For example, fungi and bacteria associations exhibiting weathering activity could be of particular interest for the sustainable use of endogenous P resources (phosphate rocks or minerals) by crops which can be critically important for organic farming or precision agriculture. Agroecological network analysis and next-generation sequencing (NGS) can be used to investigate how rhizosphere inhabitants interact with different crop species and soil chemical traits [89–91]. These types of approaches may help shed new light on the complex plant microbial community network under more realistic conditions that are closer to heterogeneous field environments. It is clear that the rhizosphere is critically important for increasing soil availability of nutrients. However, large gaps exist in our understanding of the interactions among soil microorganisms and how these organisms interact with roots to affect root growth, resistance to abiotic and biotic stresses, and overall nutrient acquisition from the soil environment. Furthermore, there has been little research conducted in perennial agricultural systems that may be more complex than annual cropping systems and may be a promising area leading to opportunities to enhance nutrient use efficiency and fruit yields in the future (Figure 2).

7. Rootstocks and Mineral Nutrition

Plants have evolved different uptake strategies to acquire mineral nutrients from heterogeneous soil environments that are spatially or temporally dynamic [92]. In general, nutrient movement across the plasma membrane of root cells occurs against the transmembrane electrochemical gradient, more negative inside the cytoplasm than the apoplast. For this reason, nutrient acquisition by roots is mainly an active process thus energy consuming involving primary (e.g., H+, Ca) and secondary active transporters (e.g., NO_3^-, PO_4^{2-}, SO_4^{2-}) [93]. Nutrient concentrations are, therefore, the result of the combined functionality of all these mechanisms. Scion nutrient concentrations are most commonly measured in leaves or fruit. Rootstock genotypes have been reported to affect scion leaf mineral concentration for apples [26,94]. Scion mineral nutrient concentration should be considered since it integrates soil availability and rootstock genotype [95]. Therefore, rootstock choice may be critical to align scion nutrient demand with environmental and soil conditions.

Although there is abundant evidence that rootstocks affect mineral nutrient concentrations in leaves and fruit, the mechanistic understanding of how these variations occur has not been fully explained. Much of the physiological and molecular research identifying the mechanisms underlying nutrient acquisition has been conducted using model plant species like *Arabidopsis thaliana* [96] as well as grain crops [97] or woody perennials like *Populus* sp. [98,99]. Several recent studies have used grapevines [100,101] and citrus [102] but, overall, nutrient acquisition has been underinvestigated in fruit crops. Among studies across multiple species, there are consistent differences in nutrient acquisition strategies and the regulation of these pathways. Furthermore, the development of phenotyping approaches for identifying variation among rootstocks in nutrient uptake and distribution to the scion would provide opportunities to identify genetic factors controlling these complex traits and make improvements to them. To reach these goals, more efforts are needed to characterize the differences in nutrient acquisition among perennial fruit species within breeding programs to select cultivars and rootstocks with elevated nutrient use efficiencies and higher quality. Furthermore, the knowledge gained in understanding the underlying mechanisms for nutrient uptake will also aid the development of sustainable nutrient-management strategies aimed at optimizing exogenous fertilizer inputs as well as increasing the production of fruit on marginal soils.

8. Root Morphology and Competition with Other Root Systems

Root architecture and spatial and temporal distribution is a critical factor affecting nutrient acquisition from the soil environment. In the last decade, there is now a stronger understanding of the associations between root traits and nutrient acquisition by plants [103–105]. This is especially true for perennial fruit species, which are often comprised of two genetically different members, a rootstock and a scion that are grafted together [94,106,107]. As a result, the relationship between production system management, soil management, tree root architecture, and the associations with growth and nutrient demand are now better understood [108]. In complex, perennial production systems, the presence of other plant species such as cover crops can affect root production, interactions with the soil, nutrient acquisition, and overall function because of changes in competition for soil resources and changes to the soil microbial community [38,109–111]. Compared to ground cover species, the root length and density of many perennial fruit species are low and these roots are often poor competitors in the soil environment. Root length densities (root length/volume) for fruit crops are typically around 2 cm cm^{-3} compared to approximately 100+ cm cm^{-3} for orchard grass species. Grass cover crops can increase root production but, without appropriate soil and water management, these cover crops can orchard yields.

Root system dynamics, such as root longevity, have been a recent focus in plant biology leading to our advancing understanding of perennial root systems (Table 1). Furthermore, root dynamics are significantly impacted by microbial partners especially arbuscular mycorrhizal fungi (AMF), which can impact both nutrient supply and root health, root architecture and function, and interactions between the rhizosphere described above. Mycorrhizal associations with roots of perennial crops have been understudied and significant opportunities are available to use new genomic technologies and imaging systems to identify beneficial species that may be commercially important at improving nutrient acquisition in soils. Root traits remain some of the most difficult to phenotype traits in plant biology and the translations of these measurements to the understanding of functional biology of roots have been limited. For a range of rootstocks of varying vigor for a single species, the total size of the root system is determined by several factors including distribution and depth. The size of root systems can be independent of the above-ground growth. One of the main challenges still remains in measuring root growth, architecture, and longevity in natural agricultural systems (Figure 2C). To further advance our understanding of differences in root traits, there needs to be a significant advancement in the capacity to collect data, provide metrics, and identify phenotypic variability in root traits that affect rootstock performance for perennial fruit production.

Table 1. Locations and fates of carbon within a tree root system.

Initial Allocation	Allocation after Primary Stage	Amount/Proportion
New white root	Brown root	All below-ground primary production
	Root cortex	Tissue is external to the stele and is shed as part of the aging process and representing a significant C input to the soil
	Root exudate	Largely unquantified but this is the source of most carbon for soil bacterial populations
	Arbuscular Mycorrhizal Fungi (AMF)	Not well quantified but may be substantial. Infection influences white root survival.
Brown root	Surviving brown root	Can survive as an isolated stele for significant periods
	Woody root	A major recipient of root carbon commonly the fate of 20–25% of root length
	Soil organic matter	A major fate of root carbon but with time lag from initial allocation to becoming soil carbon varying with root type
AMF	Soil organic matter	Potentially a major source especially for small soil pores < 8 um
Woody root	Survival until tree death then soil organic matter	A major storage compartment for C during the life of a tree

9. Root Macronutrient Uptake

9.1. Nitrogen (N)

N is largely considered to be the primary macronutrient and is a key component for amino acids and protein. N content is typically between 1.5 and 4% in leaves of perennial fruit crops. N nutrition is provided through the uptake of both inorganic (nitrate and/or ammonium) and organic forms of the nutrient by roots and then assimilation in either roots or leaves. N uptake is an active and dynamic process that is tightly regulated in response to the fluctuations in both N demand and supply. Plants must exhibit some degree of plasticity to match N uptake with demand for efficient growth and development [112].

Nitrate transport and assimilation are tightly regulated and, as such, the network controlling these processes requires plasticity to exploit spatially and temporally dynamic N pools in soil [73]. Much of our functional understanding of nitrate transport has been gained through carrying out experiments on herbaceous plants. Nitrate uptake has been reported to demonstrate two uptake pathways; a high-affinity uptake system (HATS) and a low-affinity uptake system (LATS) [96]. HATS displays saturable kinetics [113], can be both constitutive and inducible [114], and is particularly important when the external nitrate concentrations are low (generally below 0.5 mM). On the other side, LATS is not saturable and responses are linearly related to external nitrate concentrations, provided that it is higher than 0.5–1 mM [115]. Interestingly, recent pieces of evidence demonstrated that the inoculation of crop plants (i.e., maize) with N-fixing rhizobacteria can alter the physiology of nitrate uptake at the root level, highlighting that the concomitant application of conventional fertilizers and bioinoculants could not necessarily result in an enhancement in the nutrient uptake/use efficiency, particularly when nitrate is available at low concentrations at the rhizosphere [116].

Ammonium is a more direct and readily available form of inorganic N to plants since it can be directly assimilated into glutamine by ATP-dependent glutamine synthetase enzyme [113]. Similar to nitrate, there are two uptake systems; a saturable HATS, functioning when the concentration of the substrate is lower than 1 μM, and a non-saturable LATS that plays a predominant role in the uptake at a higher concentration of ammonium. At present, urea is the most used fertilizer worldwide, due to its competitive cost and its content of N per unit of mass, compared to other conventional fertilizers. Few studies have investigated the molecular bases of urea uptake in plants [117]. DUR3 encodes for the main high-affinity urea transporter, which mediates a secondary active H+/Urea cotransport [118]. Furthermore, the DUR3 gene has also been isolated in other plant species, as for instance rice and maize, albeit its transcriptional regulation appears to be species-specific [107]. Furthermore, passive uptake of urea has been also documented via the exploitation of members of the major intrinsic proteins (MIP) family of aquaporins [119]. In some soils with low pH, ammonium may represent a more significant source for N uptake. However, the transformation from urea to ammonium, and, finally nitrate means that all these transport mechanisms are required for adequate N uptake for perennial tree fruit species.

Although the majority of the research efforts to characterize N uptake have used herbaceous species under lab rather than field conditions, several studies have conducted field experiments using grapevine (Vitis vinifera L.), citrus, and cork oak (Quercus suber L.) [100,120,121]. These studies identified parallel biochemical and molecular mechanisms for N uptake as those reported for herbaceous plants. Variation in these traits for tree fruit suggests that there are opportunities to exploit this variation to enhance N use efficiencies and to optimize fruit quality but direct associations between these traits and fruit quality are poorly understood. In one example, [122] described five genes from the NITRATE TRANSPORTER 1 family that conferred nitrate uptake at low concentrations in apple. In another example, [123] reported that specific combinations of grapevine varieties/rootstocks can affect nitrate acquisition dynamics. Even though N remains one of the critical nutrients regulating growth and productivity of tree fruit species, to date, intraspecific variation in N use traits at the molecular or physiological level for perennial tree fruit species has not been adequately explored. A deeper understanding of how roots respond to exogenous N applications will contribute to improving strategies for fertilizer application and selection of rootstocks with elevated nutrient uptake efficiencies in marginal soil environments.

9.2. Phosphorus (P)

P represents up to 0.1 to 0.5% of a plant dry weight and is a key component of biological molecules such as ATP, nucleic acids and sugars. P is also involved in metabolic processes, like photophosphorylation and substrate-level phosphorylation, and it takes part in enzyme regulation and signaling cascades. Plants can take up P in the form of inorganic orthophosphate (P_i, $H_2PO_4^-$) and, within the cells, its concentration can range ranging from 1–10 mM, whilst the available concentration in the soil solution hardly reaches 10 μM unless fertigated [124]. Considering that P transport across the plasma membrane has to be energized [93], the direct uptake of the anion from the rhizosphere soil solution occurs via $2Pi:4H^+$ co-transport [125]. This process is mediated by Pi transporters, which, in plants, are encoded by a large gene family (PHT genes), within which four different sub-groups, namely PHT1, PHT2, PHT3 and PHT4, can be distinguished [126]. However, according to studies exploiting mutants and reverse genetics approaches, only members of the PHT1 sub-group seem to be involved in the uptake of Pi from the soil solution [127]. The same studies also assessed that, under stressful conditions, plants can use both high affinity and low-affinity transport systems to take up P from the soil solution. While this work supports the existing hypothesis that there are opportunities to optimize P acquisition for perennial fruit species, the development of research approaches that directly quantify P uptake and assimilation is needed before these research gaps can be addressed.

9.3. Potassium (K)

K is the most abundant cation in plant cells. K plays a fundamental role in metabolic processes like enzyme activation, transport through membranes, osmotic regulation stomatal movement, and energy transfer. Considering the huge difference in K concentration between cell cytosol and soil solution (approximately 100 mM vs. 0.1–1 mM), K uptake occurs against the concentration gradient [128]. K is transported across the plasma membrane through three types of channels (Shaker, TPK and Kir-like families) and through three types of transporters (KUP/HAK/KT, HKT and CPA families) [129]. In particular, in the case of transporters, it has been shown that, similarly to other nutrients, K has both a low-affinity and a high-affinity component [130]. There is evidence that the roots of perennial fruit species vary in their capacity to acquire K from the soil environment. For example, [92] identified variation among apple rootstock genotypes in the K uptake capacity that can affect K concentrations in the scion. Furthermore, genetic markers correlated with high concentrations of K in both leaves and fruit were recently identified [131]. Indeed, there are still opportunities to expand these research areas to further characterize the physiological differences among rootstock genotypes underlying their capacity to take up K and to understand the degree of variation that exists among other perennial fruit species.

9.4. Calcium (Ca)

For fruit production, Ca remains a critical nutrient for fruit quality and storability. Roots acquire Ca primarily from the soil as a divalent cation [132]. Ca uptake occurs in the apical zones of the roots in the first 5 mm from the root tip [133]. Ca transport into the stele of the youngest part of the root can occur either apoplastically, in the space between cells, or symplastically, through the plasmodesmata [134]. Ca movement towards the central stele is limited by the presence of a suberized Casparian band in the radial and transverse walls of the endodermis that can form a partial barrier to the radial movement of Ca to the xylem via the apoplasm. Ca must then be taken up symplastically until crossing the Casparian band [135]. The influx of Ca into the cytoplasm is thought to be mediated by ion-permeable channels located on the plasma membrane strongly favored by the electrochemical potential gradient. In addition, in several plant species, electrophysiological studies also revealed the presence of voltage-dependent Ca channels [136]. Among these, the class of hyperpolarization-activated Ca permeable channels (HACCs) has been shown to play a predominant role in the nutritional Ca fluxes at the level of root hairs [137]. Soil conditions that limit Ca uptake, even under high soil availability of this nutrient, may include water stress, low soil pH, high availability of soil aluminum and manganese, and low CEC. Once in the xylem, Ca moves through the transpiration stream. Therefore, organs that have low transpiration rates like fruit are the first to present Ca deficiencies [138]. Soil supply is not often well correlated with plant Ca concentrations. However, localized Ca deficiencies that form in the fruit of horticultural crops like apple, pear, and tomato are often not associated with soil Ca and plant factors affecting Ca distribution in above-ground tissues will be discussed later in this review.

9.5. Magnesium (Mg)

Magnesium (Mg) is an essential macronutrient to plants and it acts as co-factor for a wide range of enzymes. Mg is also the central atom in the chlorophyll molecule and is critical for photosynthesis in green plant tissues [139–141]. Mg is readily available to plants and, typically, its concentration in the soil solution ranges between µM and mM concentrations [142]. From the soil solution, Mg can diffuse passively by water flow in the apoplast of the root cortex (apoplasmic pathway) [143]; alternatively, Mg^{2+} can enter the root cells via specific transporters and then move symplastically through the plasmodesmata. However, very little information concerning the Mg transport system at the root level is available; Mg ions are thought to access the cell either through a passive movement mediated by Mg-permeable channels or through the RCA Ca channels that are permeable to a wide range of mono- and divalent cations [144,145]. Further evidence suggested that Mg uptake might be also mediated by transporters belonging to the AtMRS2 gene family [146]; in particular, a gene family composed of ten genes and one pseudo-gene, sharing homology with the yeast Mg transporter CorA [147], was annotated in the Arabidopsis genome as Mitochondrial RNA Splicing 2 (MRSA) or Magnesium Transporters (MGT) [148]. Kinetic studies highlighted that one member of the family, AtMGT7, can work as a low-affinity transporter [149], whilst the others are active in the high-affinity range of substrate concentrations [146,150]. Once take up from the soil solution, Mg is transported towards the aerial part of the plant following the transpiration stream through the xylem vessels [151]. Mg is also a phloem-mobile element and can be remobilized from leaves towards fruits, seeds, and tubers [152]. Mg and Mg-ATP are required for the loading of photosynthates into the phloem. Therefore, plants deficient in Mg may also show limitations in glucose export from leaves to sink organs [153]. In addition, several pieces of research carried out on tree species, like *Citrus sinensis* and *C. reticulata*, highlighted that Mg starvation can induce strong oxidative stress leading to the activation of the antioxidant system (e.g., thioredoxin, glutaredoxin and glutathione-S-transferase) [154]. Interestingly, [101] recently demonstrated that the ability of two different grapevine rootstocks (i.e., 1103P and SO4) to tolerate Mg deficiency relies on their ability to cope with the oxidative stress induced by the lack of the macronutrient. Similar to P, agronomic studies have dominated much of the research in Mg nutrition in perennial fruit species. From the previous example, it is clear that there is variation in tolerance to Mg deficient conditions and understanding the underlying physiological mechanisms regulating Mg acquisition and transport in perennial fruit species will help with the development of more efficient agronomic practices that enhance yields and quality of fruit.

9.6. Sulfur (S)

S is a constituent of essential amino acids, like cysteine and methionine, and is required for the synthesis of thiolic groups, which are required for the production of different metabolites involved in the resistance to abiotic or biotic stresses. Sulfate ($SO_4{}^{2-}$) is the primary source of S for plants, and $SO_4{}^{2-}$ uptake and assimilation needs to be tightly regulated and takes place through active transport [155]. Several physiological studies have highlighted that, in S-starvation conditions, the induction of HATS for $SO_4{}^{2-}$ might increase S uptake at the root level [156]. Recently, at least two transporters, namely SULTR1;1 and SULTR1;2, were identified that could be involved in this process [157]. Once taken up at root epidermis and cortex levels, $SO4^{2-}$ is moved symplastically towards the root stele. The root-to-shoot translocation is controlled by the SULTR3 and SULTR4 members of the $SO_4{}^{2-}$ transporter family; in particular, SULTR3; 5 was shown to be expressed in the vasculature bundles and its lack was related to a decreased allocation of $SO_4{}^{2-}$ to the shoot. SULTR4 transporters, on the other hand, are involved in the $SO_4{}^{2-}$ unloading from the vacuole to increase the flux of the nutrient towards the xylem [158]. At shoot level, $SO_4{}^{2-}$ needs to be unloaded from the xylem to be eventually distributed to leaves. At present, the molecular details concerning this process are still elusive, albeit unloading through ion leakage seems very probable [159]. Although S deficient conditions are rare, particularly in fertigated or irrigated fruit production, the mechanisms that regulate S transport in plants may be important under conditions that either limit soil S concentrations (sandy or weathered soils) or where there is excessive precipitation.

10. Calcium Distribution among Roots, Leaves, and Fruit

Nutrient translocation and distribution within the scion have significant implications on tree growth, fruit development, and fruit quality especially for Ca, which has long been the most important nutrient affecting fruit quality [160,161] (Figure 2D). Unlike Ca, other macronutrients are plant mobile and redistribution occurs during shorter periods of deficiencies. Therefore, much of this section has a specific focus highlighting recent studies that have focused on Ca distribution in the scion and physiological and horticultural factors affecting its distribution. Transpiration has been associated with mineral nutrient transport using mass water and C flow model for kiwi fruit, where nutrient deposition is thought to be primarily a function of both xylem and phloem transport [162]. Transpiration differences within the canopy can influence distribution and movement within the plant, with continued remobilization in the canopy, based on localized deficiencies and variation in sink demand [163,164]. Ca, however, is preferentially translocated via xylem flux. For phloem immobile nutrients such as Ca accumulation continues to organs with the highest transpiration [165].

The fundamental role of transpiration in Ca transport in fruit has been extensively described by [166–168], who illustrated that low vapor pressure deficit (VPD) and xylem conductance can affect Ca uptake into developing fruit. Under normal conditions, leaves have significantly higher Ca concentrations than fruit tissue [43] and will continue to accumulate Ca throughout the season [169]. Nutrient concentrations in leaves and fruit vary across species and among cultivars [170–173] and responses to fertilizers may also vary among rootstocks and scions [174,175].

Fruit nutrient concentrations are a function of both delivery and dilution of the overall nutrient pool in the fruit. Even with relatively high absolute delivery of Ca to the fruit, large fruit can dilute the available nutrient pool and can increase the susceptibility to Ca-related disorders. Higher transpiration rates have been reported to produce higher Ca concentrations for fruit on the outer and upper regions of the tree [176]. Once soil nutrient balance has been achieved, the primary tools for ensuring nutrient balance in apple are crop load management [177], rootstocks [178,179] and foliar applications [180]. Tree systems that promote dwarfing canopy growth, with more uniform light distribution, may promote more even mineral nutrient distributions across fruit in different regions of the canopy. The impact of rootstocks on scion fruit mineral nutrient concentrations were measured for apple [178,179] quantifying the influence of rootstock on the nutrient composition of the scion.

Most of the published research has separately evaluated Ca supply and Ca content in one specific cultivar at a time. The genetic variation in Ca concentrations between cultivars was reported by [181] for dormant, reproductive buds of bitter pit susceptible and less susceptible apple cultivars. A lower incidence of primary xylem formation in dormant buds of bitter pit susceptible cultivars indicated lower inherent fruit Ca concentration in these cultivars [179]. High Ca levels in the spur (reserve) transport tissue of less susceptible cultivars during winter contrasted with considerably lower levels in “Golden Delicious”. This was the first evidence that reserve accumulations of Ca may be remobilized into developing fruit during the season. The mechanisms underlying these observations are unknown and could provide some important insight into preventing Ca-related disorders in perennial tree fruit. This may indicate greater allocations of reserve Ca from the spur towards xylem tissue. Furthermore, results indicated a link between Ca bud content and primary xylem formation in addition to supplementary evidence of Ca transport limitations due to xylem dysfunction later in the season [182,183]. Ca transport to fruit was reported not to be determined by xylem anatomy, but the rate-limiting factor was xylem conductance at the pedicel–fruit junction at maturity that resulted in a higher Ca concentration in the pedicel than fruit [166]. This was reported to vary across apple cultivars [173]. Consistent prediction models correlating mineral analyses with bitter pit incidence are still lacking [184]. However, [185] developed a multivariate model integrating leaf N and shoot length to predict bitter pit risk in “Honeycrisp” that should be validated for different regions. There are opportunities to build on an established understanding of the contributing factors to fruit Ca-deficiencies and for the development of models that span across multiple growing regions or cultivars that can better identify fruit with greater potential for storage or higher quality.

11. Foliar Spray Supplements

Foliar applications of fertilizers (n.10 in Figure 1) are important strategies for the sustainable cultivation and production of crops. However, some of the physiological mechanisms underlying this practice, especially for Ca, are partially unknown (Figure 2D). Recent reviews by [6] have comprehensively covered much of this topic. Recent advances in technology may provide new methods to examine nutrient movement and efficiencies of foliar fertilization. For leaves, both stomata and cuticle micropores fundamentally contribute to the absorption of foliar-applied nutrients provided that plants have sufficient water supply [186]. On the other hand, information concerning the acquisition and assimilation of foliar-applied nutrients at the cell level is still scarce. It one recent example, it has been reported that NO_3^- uptake at leaf level follows the similar mechanisms underlying N transport in roots [187]. It could suggest that there are similar Ca transport mechanisms among multiple plant organs.

Foliar nutrient applications have been reported to increase fruit quality and fruit biochemistry [188,189]. However, positive results from these applications have not been consistently observed indicating that there may be limitations on scenarios where foliar applications are useful. Furthermore, the over-application of nutrients, when they are not limiting, may affect orchard productivity. Foliar Ca applications may not reduce rain-cracking in cherry [190]. Foliar applications can serve as a supplemental source of mineral nutrients including N [191] that improve tissue nutrient concentrations either within a season or, even, across seasons. Sunburn browning was lower in "Golden Delicious" and "Cripps Pink" when combinations of Ca and B were applied to fruit [192]. However, the mechanisms underlying these reductions in sunburn are not clear. Improving the efficiency of foliar nutrient applications is an ongoing concern since the acquisition of these nutrients can occur directly at the point of contact providing greater control over the delivery of nutrients to developing fruit. Timing [160,180] is a critical factor for Ca applications for bitter pit control and is closely related to surface/anatomical characteristics of tissues [184] and the Ca reserve status of the tree. However, [193] reported similar efficiencies of Ca absorption during fruit development indicating that Ca applications can be effective across the entire season.

Although previous studies have reported higher fruit Ca concentrations when foliar Ca was applied [194,195], large pre-existing Ca pools in the fruit relative to the amount applied to the fruit, challenges uptake quantification for assessing the efficacy of foliar Ca applications from sprays applied in relatively low concentrations [191]. However, recent technological developments have made it possible to better quantify nutrient absorption and distribution within plant tissues. Advancements in technology to detect localized Ca distribution include: Proton-induced X-ray spectrometry [180,196], Scanning Electron Microscopy, Wavelength Dispersive Spectrometer [179,195,197], synchrotron-based imaging and analysis and speciation at cellular or sub-cellular level [198], tracer analogs or stable isotopes [194] and Electron Dispersive X-ray (total Ca) distribution [167,199]. The relationship between Ca and bitter pit in apples was investigated through calcium extraction from cell wall tissue [200]. Analyses were performed using inductively coupled plasma atomic emission spectrometry for water-insoluble and water-soluble pectin fractions. Quantifying penetration efficiency by primarily referring to the nutrient concentration in leaves after application does not reflect the concentrations in the targeted organ and the penetration speed and depth into target tissues need to be accurately measured. For example, stable 44CaCl2 isotope movement through the peel and cortex of apple was measured and approximately 25% of the foliar application that reached the fruit surface was taken up into either the peel or the cortex [194]. This technique can be extended to include 44Ca into other Ca formulations to quantify their efficiency. Further method development will enable the re-evaluation of the role of foliar applications of mineral nutrients to fruit quality and productivity. Although new formulations for foliar applications are being continuously developed and evaluated [178,184,190,201], results have not clearly indicated whether the higher Ca concentrations in tissues, achieved with certain formulations during early development, are beneficial for quality. Improving the efficiency of foliar nutrition in the future will require the comprehensive integration of processes involved in nutrient uptake and translocation.

12. Conclusions

There is a growing recognition that improvements in soil, water and nutrient management practices across the agricultural sector will be important for addressing critical global environmental issues. To reach this goal, practices that reduce fertilizer inputs and enhance the organic matter content of orchard soils are expected to be more widely adopted for orchard systems. For perennial tree systems, nutrient dynamics that span multiple years of inputs and carryover effects from remobilization and constantly changing soil and root dynamics make it difficult to measure changes in nutrient response. Recent methodological advancements to measure nutrient fluxes in soil, rhizosphere ecology, root uptake mechanisms, plant nutrient distribution and interactions between horticulture management and mineral nutrient pools provide new opportunities to revisit old theories and to develop new management techniques to improve fruit productivity and quality. The role of microbes and management on nutrient movement, availability, and root uptake has not been fully explored and requires further research to better identify the role that these complex communities have on tree health and productivity. The physiological mechanisms underlying nutrient uptake, distribution, and cycling are well described at the molecular level for some crop species but have not fully been described for perennial fruit crops which may be derived from species with different strategies for nutrient acquisition and retention. It is clear that there is high genetic variability in these traits but further research will allow for the identification and introgression of these valuable traits that improve nutrient use efficiencies and fruit quality as well as limiting disorder development for fruit crops. Moreover, to improve nutrient use in orchards, it is evident that the availability of rootstocks particularly efficient in nutrient acquisition can undoubtedly contribute to minimizing fertilizer application as well as enhancing fruit yield and quality [202]. Advances in analytical techniques that provide opportunities for greater replication [194,203] or resolution [204] can identify the preferential acquisition of nutrients among perennial fruit rootstocks or scion cultivars. Furthermore, the use of stable isotopes and elemental analogs can be used to directly quantify nutrient uptake in soil–plant systems. Advanced phenotyping approaches can be used to characterize differences in nutrient dynamics under both field conditions and under controlled conditions. Through methodological development and working towards understanding the complex interactions that occur in perennial tree fruit cropping systems highlighted in Figure 2, better strategies for improving nutrient delivery and increasing nutrient use efficiencies will be identified during the next decade of research in this area.

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