System nutrient dynamics in orchards: a research roadmap for nutrient management in apple and kiwifruit. A review

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REVIEW ARTICLE

System nutrient dynamics in orchards: a research roadmap for nutrient management in apple and kiwifruit. A review

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Abstract

As agricultural intensification affects global environmental change, a redesign of our food production systems towards practices that replace external inputs with inbuilt ecosystem services is needed. Specifically, human-induced changes to biogeochemical flows of nitrogen (N) cycling exceed the proposed planetary boundaries, highlighting a priority area for reducing nutrient inputs in agricultural production systems. A new understanding of nutrient interactions in the complete agroecosystem will allow us to better predict and mitigate the consequences of anthropogenic environmental changes compared with a reductionist approach. Here, we review for the first time system-level nutrient interactions, particularly N, in perennial horticulture using high-producing kiwifruit and apple crops grown in New Zealand as a basis to identify critical knowledge gaps and prioritize new research. The major points identified are (1) current nutrient guidelines are from the 1980s to the early 2000s and do not take into account substantial production changes since that time; (2) few studies construct complete nutrient budgets of all sources and losses; (3) nutrient loss estimates are generally low relative to those from other agricultural land uses; (4) there is a lack of studies which address nutrient interactions between above- and below-ground food webs in perennial horticultural crops; (5) there is contradictory literature where fertilizer has been found both to increase and to decrease plant chemical signaling and defense mechanisms. New tools are emerging to improve orchard nutrient management, including advances in fertilizer application techniques, new methods to monitor plant and soil nutrients, and utilizing genetic variability to breed cultivars with improved nutrient use efficiency. To reduce adverse nutrient effects on the environment, new research is needed, addressing the relationships between carbon and nutrients and nutrient demands in modern fruit cultivars and growing systems; the nutrient balance for perennial horticultural crops considering all inputs and outputs; and interactions of the above- and below-ground nutrient flows in orchard food webs.

Keywords Biotic interactions · Fertilizer · Fruit crops · Leaching · Nutrients · Orchards · Technology

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1 Introduction

Human impacts associated with the industrial revolution and agricultural intensification have caused unprecedented global environmental changes that threaten to undermine the Earth's natural systems (Rockström et al. 2009; Steffen et al. 2015). Environment changes include climate change, biodiversity loss, soil degradation, changes in nutrient cycling, and loading with persistent toxic substances. A redesign of our food production systems is needed, towards sustainable intensification practices that replace external inputs with ecosystem services and consider whole system-based production practices in the context of the ecological landscape (Kleijn et al. 2019; Kuyper and Struik 2014; Rockström et al. 2017). International policy agreements such as 'A European Green Deal' (European Commission 2020) and 'The Paris Agreement' (United Nations 2015) promote the reduction of inputs in a range of systems including food production, providing incentives to meet reduction targets. Human-induced changes to biogeochemical flows of nitrogen (N) cycling exceed the proposed planetary boundaries (Rockström et al. 2009; Steffen et al. 2015), which highlights a priority area for reducing nutrient inputs in agricultural production systems.

By examining food production changes with a system-based approach, the benefits and trade-offs from practice changes, such as reduction of nutrient inputs, will be evaluated for all areas of the biosphere from the plant to the soil and the macro- and microorganisms. Positive and negative environmental outcomes will stem from the interactions at these boundary interfaces for different ecosystem components. Research using a complete systems approach rather than a reductionist approach allows us to better predict and mitigate the consequences of anthropogenic environmental changes (Claverie et al. 2020; Demestihas et al. 2017; Ehrenfeld et al. 2005). This is achieved by layering in research on plant-soil feedback to understand the underlying mechanisms, to predict consequences of nutrient cycling and optimization on crop productivity, disease and pest management, microbial community composition, environmental impacts, and trade-offs under a variety of conditions.

Perennial fruit and nut crops are grown on over 91 million ha worldwide and are of great economic importance in many regions as well as in global trade (FAOSTAT 2021). Within New Zealand, perennial horticultural crops are produced on over 68,000 ha, with an export market value of more than NZ$5.7 billion (Fresh Facts 2020). The largest perennial crops producing fresh fruits in New Zealand are kiwifruit and apples (Fig. 1); key industry statistics are shown in Table 1. In this review, we use kiwifruit and apple crops as case studies to examine nutritional requirements and interactions with system functions of deciduous, perennial fruit crops. Kiwifruit and apples are grown and marketed in many countries. These crops represent contrasting production systems: a vigorous, recently domesticated vine, and a low-vigor tree crop that has been domesticated for thousands of years. Therefore, they provide useful extremes to examine nutrient cycling of perennial fruit crop production systems that focus on producing high yields of high-quality fruits.

Our review takes a novel systems-level scope to examine nutrient cycling in perennial horticultural systems, focusing on N using our case study crops of kiwifruit and apple, with the aim of identifying areas to reduce external N inputs and limit environmental N emissions. To begin to address reducing nutrient inputs in perennial horticulture systems we first need to consider the nutrient requirements of fruit crops, both quantities and timing, sources and losses of nutrients in the agroecosystem, and nutrient interactions with the food web of the orchard ecosystem. We conclude by identifying key research gaps limiting our understanding of nutrient dynamics in these systems, and novel technologies for smart fertilization practices.

2 Current practice

Current plant nutrient guidelines in New Zealand kiwifruit orchards are based predominantly on earlier studies of two commercial cultivars, the green-fleshed kiwifruit (*Actinidia chinensis* (A. Chev.) C. F. Liang et A. R. Ferguson var. *deliciosa* 'Hayward') and gold-fleshed kiwifruit (*Actinidia chinensis* Planch. var. *chinensis* 'Hort16A') (Mills et al. 2008, 2009; Morton and Woolley 2011; Smith et al. 1987), which did not consider yield responses to nutrient applications. However, vine yield has increased significantly since these studies were carried out, owing to significant changes in management practices, for example changing from 'T' bar to pergola canopy systems and the introduction of a new gold-fleshed kiwifruit cultivar (*Actinidia chinensis* var. *chinensis* 'Zesy002' to replace 'Hort16A' which was decimated by the disease *Pseudomonas syringae* pv. *actinidiae* (Psa) (Ferguson 2015). The story is just as complex for apples, as the work was carried out in the 1980s and 1990s, based on studies of older cultivars like 'Golden Delicious', 'Braeburn', and 'Cox's Orange Pippin' growing as widely spaced, freestanding trees in two regions (Goh and Haynes 1983; Palmer and Dryden 2006). The impacts on nutrition of the introduction of new cultivars like 'Scifresh' and 'Scilate' on dwarfing rootstocks, location, climate, and two-dimensional trellis growing systems with higher tree densities have not yet been considered.

Nutrient applications in New Zealand orchards are based on local industry knowledge, leaf and soil testing, nutrient removal from the orchard, and plant characteristics like age, cultivar, and performance. Leaf analyses are carried out in spring for kiwifruit and in mid-summer for apple; however, it can be difficult to gain a clear picture of plant nutrition because of variability between leaves and the importance of

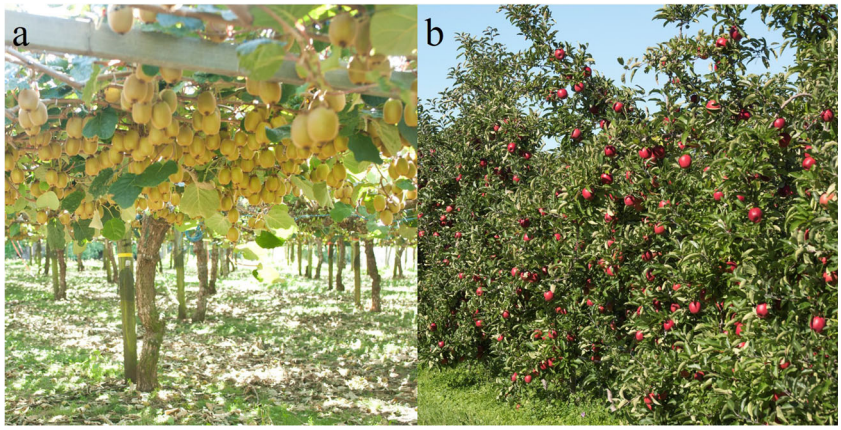

Fig. 1 The largest perennial crops producing fresh fruits in New Zealand are (**a**) kiwifruit and (**b**) apples. Photographs by The New Zealand Institute for Plant and Food Research Limited.

nutrient reserves for perennial fruit crops. Leaf concentrations of key mineral nutrients in apple and kiwifruit change throughout the season. They are influenced by the phenological stage of the shoot, the presence of fruit, and the mobility of the mineral nutrient in the plant. High concentrations of phloem-mobile macro-nutrients (e.g. N, phosphorus (P), potassium (K), magnesium (Mg)) are found in leaves pre-flowering, whereas leaf concentrations of phloem-immobile minerals such as calcium (Ca) are low (Smith et al. 1987). After flowering through to harvest N, P, and K leaf concentrations tend to decline in both apples and kiwifruit as the minerals are remobilized from the leaves and move to other developing sinks e.g. fruit and roots and the N is diluted through leaf growth (Nachtigall and Dechen 2006; Smith et al. 1987). In contrast, concentrations of minerals with intermediate to low phloem mobility (e.g. Ca, manganese (Mn), iron (Fe)) increase in leaves throughout the season, as they accumulate via the xylem in the transpiration stream and remain in the leaf. Leaf concentrations of nutrients can be affected by the presence/absence of fruit. For example, P increases slightly in 'Hayward' kiwifruit leaves towards the end of the season in non-fruiting shoots but declines in the presence of fruit (Smith et al. 1987). Nutrient concentrations in leaves can also be affected by scion and rootstock cultivar combinations. For example, Mg concentrations increase through the season in 'Fuji' and 'Golden Delicious' leaves but remain constant in 'Gala' leaves (Nachtigall and Dechen 2006). Combining a 'Gala' scion with the rootstock G890 elevated mineral nutrient uptake compared with that in 'Gala' scions combined with G41, M9, and B9 rootstock genotypes (Valverdi et al. 2019).

In addition to leaf analysis, fruit and soil mineral analyses are sometimes used as a guide for nutrient application, especially focusing on fruit quality where Ca concentration can affect harvest quality and storage of the fruit (Torres et al. 2017). In apples, the nutrient concentration required for healthy fruit growth is different depending on the cultivar, growth phase, and also within an orchard (Palmer and Dryden 2006). Orchard soils are generally sampled using a single test in winter, although these analyses do not provide a good overview of the spatial variability across orchards and within the root zone (Srivastava and Malhotra 2017).

Nutrient removed from the system each year is calculated from harvested fruit, growth, and prunings plus an amount to cover environmental losses (see Section 4.2). For example, in 'Hayward' kiwifruit orchards (yield 40 t ha^{-1}), some 27–48 kg N ha^{-1} is removed as fruit, and growers typically apply 75 to 100 kg N ha^{-1}, although N inputs across New Zealand kiwifruit orchards range from 0 to 226 kg N ha^{-1} (Carey et al. 2009; Morton 2013). In New Zealand apples (yield 70 t ha^{-1}), N loss from harvested fruit is around 24–36 kg N ha^{-1} depending on the cultivar (Palmer and Dryden 2006) with average

Table 1 New Zealand industry statistics for apples and kiwifruit.

Statistic	Apple	Kiwifruit	Source
Area grown (ha)	10,396	12,905	Fresh Facts (2020)
Export market value (NZ$)	$876 million	$2.5 billion	Fresh Facts (2020)
Average yield (t ha^{-1})	65	44.5	Fresh Facts (2020)
Maximum yield (t ha^{-1})	170–180	74	Thorp et al. (2011); Tustin and van Hooijdonk (2016)
On-orchard costs (NZ$ ha^{-1})	$29,400	$38,900	ANZ (2019); Journeaux et al. (2019)
Average orchard gate return (NZ$ ha^{-1})	$67,200	$107,142	Fresh Facts (2020); Journeaux et al. (2019)

applications around 30–80 kg N ha^{-1} (Goh and Haynes 1983; Morton 2013). However, industry production practices and yields have changed since these earlier publications and there have been no more recent studies of these crops in New Zealand.

As fertilizer is a relatively inexpensive component of orchard management inputs, growers ensure non-limiting supplies of nutrients are readily available to plants. In some cases, this may lead to inefficient use of nutrients (Li et al. 2019). This can have a wide range of consequences on plants (yield, fruit quality, vigor, and pest and disease susceptibility) as well as on the orchard ecosystems and the surrounding environment (Marsh et al. 1996; Morton 2013; Weinbaum et al. 1992).

3 Plant nitrogen dynamics

Nitrogen is a highly mobile nutrient, cycling rapidly through the plant, soil, and environment. Plants have a high demand for N and it combines with carbon to form essential compounds like amino acids, proteins, nucleic acids, and chlorophyll. Plant roots actively take up N from the soil as nitrate; however, they are also able to assimilate ammonium ions. Once nitrate is taken up by roots, it is generally reduced to ammonium in the roots, although it can be transported to leaves and then reduced. For example, half of the nitrate absorbed by 'Hayward' kiwifruit roots was reduced in the roots (Ledgard and Brier 1991). Uptake of N from roots to leaves is via the xylem; however, retranslocation between sources and sinks within the plant is primarily via the phloem (Guak et al. 2003; Ledgard and Brier 1991). In apples, new growing tissues in spring, particularly leaves (30–50% of plant N) and fruit (18% of plant N), are the major sinks for N in trees of all ages (Batjer et al. 1952; Forshey 1963; Neilsen et al. 2001b). Prior to leaf fall, up to 50% of the N in leaves is withdrawn and stored in the woody framework of plants. This is essential to support new growth in spring before the canopy and root system are able to fully support plant demands. If N is applied too early in late winter or early spring before the plants come out of dormancy, the plant roots are unable to take it up leading to fertilizer loss to the environment through leaching and volatilization (Neilsen and Neilsen 2002). Breaking of dormancy can vary significantly across cultivars of single crops, for example, the timing of the generation of root pressure in kiwifruit grown in New Zealand can vary between late July to October in different kiwifruit varieties (Clearwater et al. 2007).

3.1 Nitrogen responses

Nitrogen deficiency, or over-supply, can have negative impacts on fruit productivity and quality. Insufficient N can reduce leaf expansion and shoot growth and reduce individual leaf photosynthesis, resulting in limited assimilation for fruit growth or storage to support flowering in the following season (Buwalda and Meekings 1993). However, the high mobility of N within the plant, the ability of the plant to store and remobilize N over the short term, and changes in growth rates in response to low N availability can often mask N deficiency in the orchard, which is typically monitored using leaf N analysis (Buwalda and Smith 1990). For example, long-term N withholding trials on 'Hort16A' kiwifruit vines on an orchard in Te Puke, New Zealand, over 6 years did not affect leaf N levels, but the impact of reduced N supply could be observed through reduced fruit size, increased fruit dry matter content and advanced fruit maturity (Barnett pers. comm.). Soil type, fertilizer history, and seasonal weather patterns also make orchard trials designed to understand plant N requirements difficult, and long-term trials are required.

Excessive N application can enhance shoot growth (Buwalda and Meekings 1993), which competes with fruit for assimilates. Vigorous shoot growth can create shade, which can adversely affect fruit quality (Grant and Ryugo 1984; Snelgar et al. 1998; Tombesi et al. 1993) requiring more shoot biomass removal by pruning (Boyd 2012; Morton 2013). This then may result in increased wound generation from extra pruning cuts or shoot breakages, which result in additional sites for infection with pathogens like *Pseudomonas syringae* pv. *actinidiae* Biovar 3 (Psa) in kiwifruit (Ferrante et al. 2012) and *Neonectria ditissima* in apple (Amponsah et al. 2015; Dryden et al. 2016), and other pathogens.

High N applications can also affect fruit quality. Increasing annual rates of N up to 200 kg N ha^{-1} resulted in reduced apple flesh firmness and red color, whilst increasing from 50 to 200 kg N ha^{-1} reduced apple total soluble solids contents (Fallahi et al. 2010; Nava et al. 2008; Neilsen et al. 2009). In Italy, six years of high N application to kiwifruit resulted in fruit starting to soften earlier in storage (Vizzotto et al. 1999) and high N application to 'Hayward' kiwifruit in California caused fruit to soften more rapidly in storage (Johnson et al. 1997).

It has also been reported that excessive N can cause fruitstalk wither and premature softening of kiwifruit in New Zealand (Sher and Yates 1992). However, Boyd (2012) found that this was not consistent over multiple years. Higher than standard N applications resulted in vines that were less productive, the fruit maturity was delayed, and as a result, the fruit had a higher incidence of low-temperature breakdown in storage (Boyd 2012). Maximum vine growth does not equal maximum productivity or maximum fruit quality in crops. This highlights the subtlety needed for N management in perennial trees and vines, unlike in pastoral systems where vegetative growth is the prime goal.

3.2 Prioritized knowledge gaps

Much of the information on nutrient requirements of apples and kiwifruit is over 30 years old. Since these studies were carried out, the yield and fruit quality produced in New Zealand apple and kiwifruit orchards have been transformed by the introduction of new cultivars and management techniques. To update our knowledge of plant nutrition and improve practices in kiwifruit and apple orchards, a number of gaps in our knowledge need to be filled (Fig. 2). These include improved understanding of the relationship between plant carbon fixation and nutrient availability, particularly N, which could improve both productivity and sustainability outcomes in orchards. The majority of the historical work has been carried out by looking at crop responses to fertilizer regimes over one or more seasons. Whilst this research has helped us narrow down our fertilizer requirements, the large gains now are to be made through targeted nutrition focused around the right time in the season to match that cultivars requirements, application to ensure the nutrient is supplied to the right tissues at the right amount to limit loss while maximizing yield. To enable this, we need to extend our knowledge of nutrient dynamics in perennial fruit crops to a seasonal view of nutrients throughout plants including their root systems (Fig. 2). In order to develop better nutrient management techniques, we need to develop new systems that can non-destructively monitor plant nutrient uptake, use, and losses in real-time which will allow us to fine-tune our fertilizer programs. New knowledge in these areas, together with more targeted application methods, should lead to a more sustainable approach to nutrient inputs while maintaining or increasing plant productivity and enhancing environmental outcomes.

4 Sources and losses of nutrients

4.1 Nutrient sources

In perennial orchard systems, nutrients accumulated in the fruit are derived from the remobilization of storage reserves within the plant and nutrient uptake from external nutrient sources. Spring growth first begins with the remobilization of stored nutrients followed by rapid root growth and external nutrient uptake after breaking dormancy (Neilsen et al. 2001b;

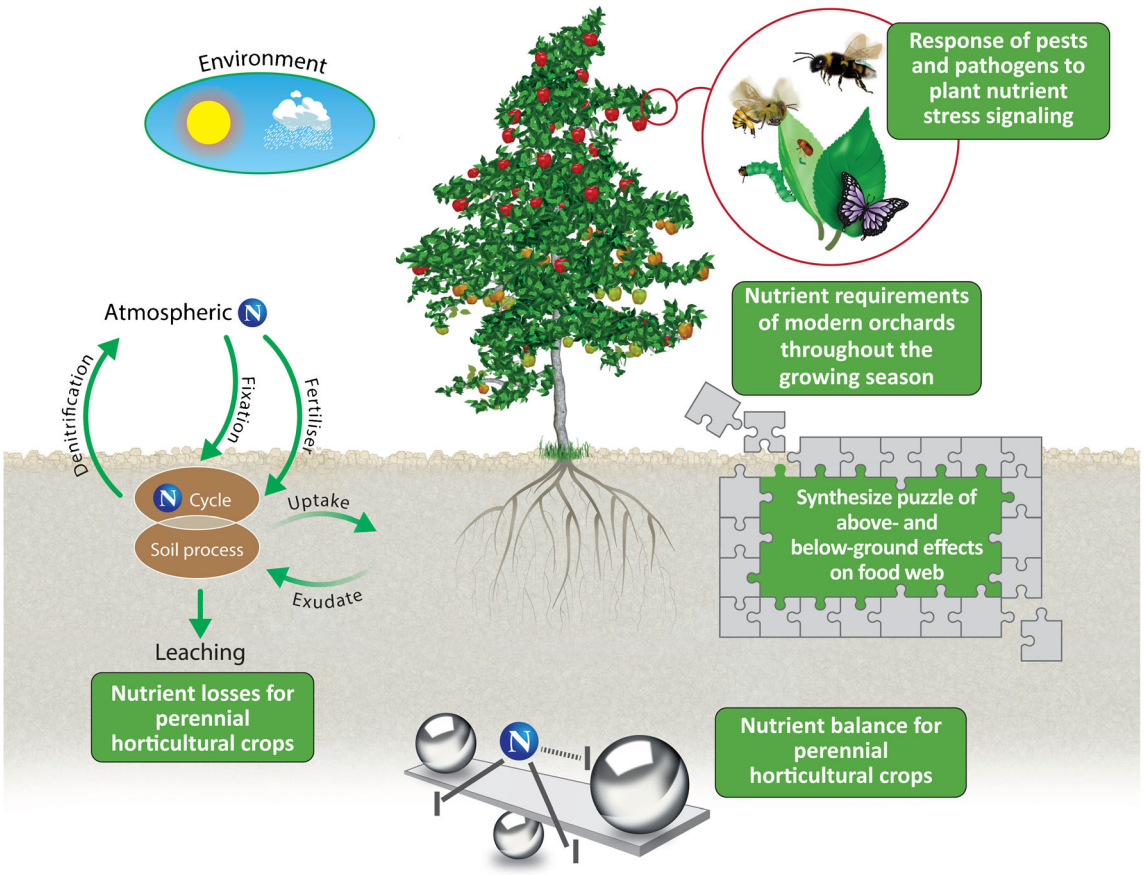

Fig. 2 Key research gaps identified in understanding system nutrient dynamics in orchards include: understanding the response of pests and pathogens to nutrient stress signaling (Section 5), knowledge of nutrient requirements in modern cultivars and growing systems throughout the growing season (Section 3), synthesizing the puzzle of above- and below-ground effects on food web interactions (Section 5), quantifying nutrient losses in orchards (Section 4), and determining nutrient balances for perennial horticultural crops (Section 4).

Tagliavini and Scandellari 2007; see Section 3). Plants acquire nutrients from external sources through root uptake of soil nutrients or leaf uptake of foliar nutrient applications. Soil-available nutrients are derived from mineral fertilizer application, organic amendments, rainfall, irrigation water, mineralization of soil organic matter, and decomposition of orchard leaf litter, prunings, and groundcover plants.

Few studies have constructed complete orchard nutrient budgets in apples or kiwifruit comparing contributions from all sources. Atucha et al. (2011) calculated N budgets including external inputs and soil fluxes for an apple orchard in New York, USA, using different groundcover management and fertilizer inputs. However, this study did not quantify the remobilization of tree N reserves. In fertilizer-applied treatments, external inputs accounted for 52–57% of the N input, while soil fluxes from soil mineralization and plant litter decomposition accounted for 43–48% (Atucha et al. 2011). This indicates the importance of soil nutrient cycling to nutrient uptake in orchards. Greater understanding of the quantity and timing of nutrient availability from soil fluxes is needed to reduce external nutrient inputs to move towards minimal input horticulture.

Nitrogen use efficiencies, expressed as the quantity of the N removed in the crop as a percentage of fertilizer N applied, are generally quite low for fruit trees compared with other agricultural land uses owing to an over-application of fertilizer compared with crop requirements (Wang et al. 2016; Weinbaum et al. 1992). Field studies quantifying nutrient uptake using ^{15}N isotopic tracer methodology report fertilizer use efficiencies of <17 to 32% in apples grown in Canada and Australia (Neilsen et al. 2001a; Neilsen et al. 2001b; Tan et al. 2021) and 48 to 53% in kiwifruit grown in New Zealand (Ledgard et al. 1992). These low fertilizer uptake efficiencies indicate that applied nutrients could be accumulating in the soil, or be vulnerable to losses from the orchard ecosystem. Indeed, Ledgard et al. (1992) report soil retention of 18 to 22 % of ^{15}N-labelled fertilizer applied to kiwifruit and an apparent loss of 26 to 32 % of fertilizer N after one growing season. Thus, there is room for improvement in the management of mineral fertilizers to better match crop requirements through targeted nutrition based on new knowledge of seasonal nutrient requirements of modern perennial fruit crop cultivars and growing systems (see Section 3.2).

The rate of soil organic matter mineralization and nutrient release varies with soil type, land use history, temperature, and soil moisture (Curtin et al. 2012). The contribution of mineralization to crop N supply may range from <20 to >200 kg N ha^{-1} (Cabrera et al. 1994) depending on the quantity of mineralizable organic N in the soil and environmental conditions that control the rate of mineralization. New Zealand soils have large stocks of soil organic matter relative to global soils (Tate et al. 1997). Soil organic carbon and nitrogen stocks to 1-m depth averaged 162 t C ha^{-1} and 15.5 t N ha^{-1} in a survey of kiwifruit orchards in the main growing regions of Bay of Plenty and Waikato in New Zealand (Gentile et al. 2021). Soil organic carbon stocks in apple orchards in New Zealand's largest apple production region in Hawke's Bay averaged 132 t C ha^{-1} to 1-m depth (Gentile et al. 2016). Several chemical, physical, and biological measures have been proposed as indicators of potential mineralizable N from soil (Curtin and McCallum 2004; Sharifi et al. 2007) including hot water-extractable N, which is a sensitive indicator of potentially mineralizable N in New Zealand soils (Curtin et al. 2017). Kim et al. (2011) found hot water-extractable C was a predictor of N mineralization in New Zealand apple orchard soils. They concluded that orchard C management to increase labile organic matter was a greater driver of soil N mineralization than temperature and moisture environmental conditions. Field rates of N mineralization may be predicted using models that incorporate the potential mineralizable N pool and rate constants for soil temperature and moisture content (e.g. Dessureault-Rompré et al. 2012; Paul et al. 2002).

Nutrients are internally recycled through the decomposition of plant biomass in the orchard system via mowed groundcover and tree leaf litter and prunings. Groundcover plants show rapid rates of decomposition and nutrient release within the growing season (Tagliavini et al. 2007; Tutua et al. 2002). Tutua et al. (2002) report the N half-life of a ryegrass and clover groundcover was 50–110 days in a New Zealand apple orchard. This groundcover could provide a net input of N to the orchard system if the species mix includes legumes to add N through biological N fixation. A study on N_2 fixation of groundcover plants in a Canterbury, New Zealand, apple orchard found biological N fixation ranged from 112 to 143 kg N ha^{-1} over 2 years (Goh and Ridgen 1997; Goh et al. 1995). Clover groundcover N_2 fixation in New Zealand kiwifruit orchards was estimated to be 28 kg N ha^{-1} $year^{-1}$ (Smith et al. 1988). In contrast to groundcover plants with high N concentrations, orchard crop plant leaf litter and prunings have higher C:N ratios and slower decomposition rates. Apple leaf litter decomposition first has a phase of net N, P, and S immobilization for a period of 6 months to 1 year, and then shows a net release of N with 30 to 40 % of the initial litter N content released in the second year (Han et al. 2011; Tagliavini and Scandellari 2007; Tagliavini et al. 2007). A field study of kiwifruit pruning wood decomposition including leaves showed only 9 % of the N content was taken up by the following crop after 2 years (Ledgard et al. 1992).

Nutrient release rates from organic fertilizers and amendments such as composts and mulches can vary widely depending on the quality of the amendment. Parameters such as N, C:N, lignin, and polyphenol contents have all been suggested as being influential in determining the timing of N release (Cassity-Duffey et al. 2020; Lazicki et al. 2020; Palm et al. 2001). Nutrient release will also be modified by climate. Predicting the quantity of nutrients available from different

organic sources, and what is locally available for our perennial production systems, is a research gap.

4.2 Nutrient losses

Nutrients may be lost from perennial horticulture systems via leaching, runoff, gaseous emissions, and crop removal at harvest. Compared with other agricultural land uses, N leaching losses under perennial horticulture crops in New Zealand are relatively low (Journeaux et al. 2019). Annual N leaching rates from previous New Zealand studies are shown in Table 2 and range from 1 to 33 kg N ha^{-1} $year^{-1}$ in apple production and 3 to 39 kg N ha^{-1} $year^{-1}$ under kiwifruit. Reported values for the N leaching footprint of apples and kiwifruit in New Zealand are very similar despite slightly higher inputs of fertilizer under kiwifruit production (see Section 2). There have been a few published field measurements of N leaching in perennial horticulture (Clothier et al. 2012; Goh and Haynes 1983; Green et al. 2007; McIntosh 2009). However, the majority of the leaching estimates are derived from various research and nutrient management models. The N leaching values between direct measurements and modelled estimates are generally comparable.

The occurrence of nutrient leaching is determined by drainage from rainfall and irrigation events (Neilsen et al. 2008) that are seasonally focused in temperate climates (Riga and Charpentier 1999), whereas the quantity of nutrients leached is also influenced by nutrient inputs (Neilsen et al. 2008) and orchard management strategies (e.g., orchard design, planting density and sward management). Management strategies to decrease nutrient leaching losses include decreasing the amount of nutrients applied, optimizing the timing of applications, and applying woody mulches (Merwin et al. 1996; Neilsen et al. 2008). In New Zealand scenarios, Journeaux et al. (2019) found a minimal change in N leaching losses by eliminating N fertilizer use, and greater N leaching losses when compost or clover understory crops were used in place of N fertilizer inputs owing to lower crop nutrient extraction and higher N mineralization. They suggest that reducing fertilizer inputs offers little impact on nutrient losses relative to an already well-managed fertilizer regime in perennial horticulture crops. There is a need to improve the understanding of leaching losses in modern orchard systems.

Nutrient losses from runoff are assumed to be minimal in New Zealand perennial horticulture production systems because of the typically flat terrain in orchards and grassed alleyways, which reduce erosion risk. However, this may change if perennial horticulture expands to more sloping land. There are few studies reporting runoff nutrient losses from perennial horticulture in New Zealand. Modelled P losses for perennial horticulture in the Hawke's Bay region ranged from 0.13 to 0.58 kg P ha^{-1} $year^{-1}$, with 55–78% of this loss occurring via leaching and drainage instead of runoff. Modelled runoff P losses in the Gisborne region ranged from

Table 2 The nitrogen-leaching footprint of kiwifruit and apple crops grown in New Zealand.

Crop	Nitrate leached (kg N ha^{-1} $year^{-1}$)	Region	Measurement method	Reference
Apples	33	Canterbury	Aldunum tension lysimeters	Goh and Haynes (1983)
Apples	2–12	Canterbury	Modelled for a range of regional soils and climates	Green and Clothier (2009)
Apples	1.4–12.4	Hawke's Bay	Modelled for a range of regional soils and two irrigation regimes	Green et al. (2012)
Apples	9–14	Hawke's Bay	Drainage fluxmeters	Clothier et al. (2012)
Apples	5.2	National, major growing regions	Modelled for a range of soils	Clothier et al. (2012)
Apples	3–18	Tasman, Waimea Plains	Modelled for a range of regional soils	Fenemor et al. (2016)
Apples	9–24	Hawke's Bay	Modelled for a range of regional soils	Archer and Brookes (2018)
Apples	5.4	National	Modelled industry average	Journeaux et al. (2019)
Kiwifruit	39	Bay of Plenty	Drainage fluxmeters and modelling	Green et al. (2007)
Kiwifruit	<15	Bay of Plenty	Modelled for a range of regional soils	McIntosh (2009)
Kiwifruit	5.8–9.2	Bay of Plenty	Groundwater monitoring bores	McIntosh (2009)
Kiwifruit	3–15	National, major growing regions	Modelled for a range of regional soils	Deurer et al. (2011)
Kiwifruit	4–27	Gisborne, Poverty Bay flats	Modelled for a range of regional soils	Gentile et al. (2014)
Kiwifruit	9–23	Hawke's Bay	Modelled for a range of regional soils	Archer and Brookes (2018)
Kiwifruit	6.4	National	Modelled industry average	Journeaux et al. (2019)

0.1 to 1.0 kg P ha^{-1} $year^{-1}$ for kiwifruit, grape, and citrus production (Gentile et al. 2014). Similarly, Clothier and Green (2017) modelled the annual New Zealand national average for vineyard P losses from combined leaching and runoff to be 0.25 kg P ha^{-1} $year^{-1}$.

Soil N can be converted to gases and lost to the atmosphere by denitrification and NH_3 volatilization. There have been no measurements of gaseous N losses under perennial horticulture in New Zealand. An international meta-analysis of nitrous oxide (N_2O) emissions in perennial fruit trees found annual emissions ranged from −0.116 to 26 kg N ha^{-1} $year^{-1}$ (Gu et al. 2019). Cumulative N_2O emissions also increased linearly with N fertilizer rates. Interestingly, N_2O emissions were higher with organic than synthetic fertilizers (Gu et al. 2019). Similarly, Kramer et al. (2006) found that N_2O emissions were the same between organic and conventional apple orchards in Washington State, USA, but that N_2 losses were greater from the organic orchard, indicating larger total gaseous N losses. These results suggest that increased carbon availability with organic fertilizers may stimulate denitrification N losses. In contrast, Fentabil et al. (2016) found that surface-applied wood mulch reduced N_2O emissions in a Canadian apple orchard even though soil labile organic carbon increased.

Gaseous emissions from apple orchards show high temporal and spatial variability in the international literature. N_2O emissions are higher during the summer growing season in climates without freeze-thaw cycles (Riga and Charpentier 1999; Swarts et al. 2016) and pulses of N_2O occur after N fertilizer applications and summer rainfall or irrigation (Fentabil et al. 2016; Pang et al. 2009). Pang et al. (2009) found N_2O emissions increased closer to the tree row and band of fertilizer application in an apple orchard in China, whereas Swarts et al. (2016) found N_2O emissions in Australian apple orchards were greater in the grassed alleyway than the tree line, which may have been due to higher carbon inputs or poorer soil structure in the alleyway. While there are a few international studies quantifying N_2O emissions in apple orchards, we found no published studies measuring N_2O emissions under kiwifruit production.

4.3 Prioritized knowledge gaps

Constructing a complete N balance for New Zealand horticultural crops would enable us to quantify all N fluxes for the entire orchard system (Fig. 2). These balances need to be considered for different cultivars, management systems, and growing regions, to be able to examine nutrient losses (leaching, runoff, gaseous emissions) and the net balance of inputs and outputs to determine if production is maintaining or mining nutrient contents in the soil. Secondly, predicting the nutrient availability and release from soil mineralization and organic amendments in different growing regions is critical to quantify the amount and timing of availability of nutrients from these sources to better match nutrient applications with crop requirements. Lastly, there are no published data on N_2O emissions and few field measurements of nutrient leaching in perennial horticulture in New Zealand (Fig. 2). Robust field data for these nutrient losses in relation to other temporal variables would improve environmental monitoring and reporting (e.g., greenhouse gas inventory reporting) and identify key areas where losses could be reduced. Identification of high-risk leaching periods and the nutrient source (e.g. fertilizer, soil organic matter mineralization, compost) would allow management-specific interventions to be developed to reduce nutrient leaching.

5 Nutrient interactions with the food web

A food web represents all the food chains in an orchard ecosystem, over all trophic levels. Understanding the food web structure is important for understanding nutrient cycling, system stability and recovery, and population and community dynamics (de Vries and Wallenstein 2017; Fagard et al. 2014; Maaroufi and De Long 2020; Whalen et al. 2013). The quantity and diversity of organisms in a soil food web determine nutrient availability to plants (e.g., Lakshmi et al. 2020; Whalen et al. 2013). Therefore, soil food webs are critical to the orchard system dynamics including nutrient management and, vice versa, nutrients can have complex effects on food webs including interactions between biotic and abiotic factors (Bengtsson et al. 2005; Tuck et al. 2014). To understand the impact of nutrients on interactions over organizational hierarchies, we need to consider competition and trophic interactions at the community level and trade-off dynamics, such as competition, growth and plant immunity, influencing processes at the ecosystem level (Gagic et al. 2017; Johnson et al. 2016; Keurentjes et al. 2011; Tao et al. 2017; van Gils et al. 2016). There are many facets of how nutrition at the orchard scale could change the hierarchy of the food web and increase or decrease resource competition among species (Keurentjes et al. 2011; Van der Putten et al. 2013).

Existing research addresses nutrient feedback loops on food webs, and food web structure effects on nutrient dynamics, primarily from ecological theory and grassland and agriculture systems (e.g. Tsiafouli et al. 2015; Van der Putten et al. 2001) with fewer studies in perennial horticulture (see Lago et al. 2019 for the detrital foodweb under kiwifruit). Biotic and abiotic processes influencing nutrient availability can affect food web stability (DeAngelis et al. 1989; Huxel and McCann 1998; McMeans et al. 2015), and shifts in nutrient resource quality can alter trophic interactions (Koricheva et al. 1998). These influences are little studied for perennial horticultural settings but have a large potential to play important roles in the trophic interactions with nutrition under

horticultural management. Nutrient management practices in high-intensity land-use trend toward low complexity food webs (Tylianakis and Binzer 2014) with changes in above- and below-ground food webs from top-down and bottom-up effects. These food web changes alter the dynamics of organic matter decomposition and nutrient cycling and therefore affect plant nutrition, which in turn affects above- and below-ground food webs. Existing soil nutrient pools, or nutrient stores in plant biomass, can buffer changes in organic matter nutrient release (Buchkowski et al. 2019).

5.1 Type of nutrient applications

The form (e.g., organic versus inorganic) of nutrient application can have different outcomes and flow-on effects in the food web and ecosystem. For example, Rowen et al. (2019) reviewed studies comparing manure and synthetic fertilizer treatments in a variety of cropping systems, including apple production, and found animal manure influenced pest control in two different ways. Manures had bottom -up effects on prey suppression by changing plant nutrient concentrations and altering plant defense chemical production. Additionally, manures showed top-down effects on biological control by improving the soil habitat for predators through increased soil organic matter and water retention. Other studies show that adding compost as a mulch in apple orchards creates a more diverse ecosystem and is likely to have beneficial impacts on orchard sustainability (Brown and Tworkoski 2004; Doran 2002; Yao et al. 2005). Lago et al. (2019) found that intensive, conventionally managed kiwifruit orchards had less complex soil food webs, which were capable of rapid mineralization of soil organic matter. However, less intensively managed kiwifruit soils using compost amendments supported a more diverse soil food web, including organisms with roles in improving soil structure and incorporating soil organic matter, resulting in higher C and N retention (Lago et al. 2019).

While nutrient release from the decomposition of organic matter in mulch can enhance soil quality (TerAvest et al. 2011), mulching might also affect pest and disease management at other trophic levels. Miñarro et al. (2009) concluded that a change from herbicide use to mulching or mechanical weed control may have significant effects on taxonomic groups of soil-dwelling predators. Adding organic material to the soil of an apple orchard significantly affected arthropod abundance, leading to more predators and fewer herbivores, but no effect was observed on rates of apple scab (*Venturia inaequalis*) infection (Brown and Tworkoski 2004). Damavandian (2000) found that straw mulch in apple orchards can affect migration in the subterranean apple aphid (*Eriosoma lanigerum* (Hausmann)). A small change on one trophic level has the potential to affect higher trophic levels, and ultimately, propagate through the entire food web (Chen and Wise 1999). This results in a balance of trade-offs between beneficial and pest components of the food webs, dependent on management practices including nutrient applications. In a study by Mathews et al. (2002), the application of mulch to the soil surface affected soil detritivores, herbivores, and predators, as well as the host plant in a *'Golden Delicious'* apple orchard. Thus, the type of nutrient application can affect the food web at several trophic levels and have different implications for the nutrient effects on an orchard ecosystem as a whole.

5.2 Above- and below-ground food webs

Most food web studies often study a single part of the system such as the above-ground canopy food web, effect of nutrients on herbivory, or parts of the below-ground food web (Koricheva et al. 1998; Poveda et al. 2007; Ramirez et al. 2018; Van der Putten et al. 2001). However, these subsystems depend on and interact with each other (A'Bear et al. 2014; Hannula et al. 2019; Poveda et al. 2007; Van der Putten et al. 2001; Yang et al. 2020). The lack of studies addressing the interactions between above- and below-ground food webs in orchard crops has been noted (Demestihas et al. 2017; Mercado-Blanco et al. 2018). In the international literature, most of the studies addressing interactions between above- and below-ground food webs are in annual crops or grasses (Heinen et al. 2020; Heinen et al. 2018; Masters et al. 2001; Pineda et al. 2017; Zhu et al. 2018). Nutrient exchange intimately links above- and below-ground biota (van der Heijden et al. 2008) and more sophisticated orchard models are needed for studying above- and below-ground interactions, particularly in perennial systems (Demestihas et al. 2017; Mercado-Blanco et al. 2018; Ramirez et al. 2018; Van der Putten et al. 2001).

Interactions between plants, insects, and microbes are mediated in many cases through chemical communication. A myriad of responses by both herbivore and host can be driven by changes in nutrient availability (Gershenzon 1984; Mur et al. 2017). Nitrogen availability can both positively and negatively affect a pathogen's infection strategy, and alter host plant defense mechanisms (Sun et al. 2020). Depending on the system or chemical compound, fertilizer inputs can result in increased or decreased quantities of plant secondary metabolites (Gershenzon 1984; Jamieson et al. 2017). These changes to plant chemical signals may be in the form of altered ratios of volatile compounds, cessation of some compounds emitted, or the production of new compounds (El-Hawaz et al. 2018; Gouinguené and Turlings 2002). Meta-analyses show that N inputs decrease foliar concentrations of carbon-based plant secondary compounds and increase several measures of insect herbivore performance including development time, biomass and growth rates (Koricheva et al. 1998; Li et al. 2016). Nitrogen fertilization of field crops often stimulates insect populations as a result of increased plant consumption

and higher food utilization rates (Altieri and Nicholls 2003; Muthukrishnan and Selvan 1993). Despite this initial negative outcome of stimulating herbivorous insect populations, N fertilizer effects can flow onto connected trophic levels, resulting in improved outcomes for parasitoids, for example, increased parasitoid hatch rates and lifespan (Aqueel et al. 2015).

Below-ground food web communities, particularly microbes, influence plant nutrient uptake. The structure and function of the soil microbiome are dynamic and are influenced by multiple biotic and abiotic factors such as plant host, environmental conditions, soil type, seasonality, and management practices (Lakshmanan et al. 2014; Whitehead et al. 2021). Fertilization decreases microbial community diversity and shifts below-ground food webs to bacterial rather than fungal dominance (Bardgett et al. 1999; de Vries and Wallenstein 2017; Rahman and Sugiyama 2008). The ratio between bacterial and fungal community dominance is correlated to the rates of C and N cycling processes (de Vries and Wallenstein 2017). Additionally, the size, number of densely connected networks, and number of connections between networks in below-ground food webs are reduced with conventional fertilizer use (de Vries and Wallenstein 2017). Further research is needed to elucidate the effects of nutrient additions on below-ground food web functions in orchard ecosystems.

5.3 Prioritized knowledge gaps

There is a lack of synthesis of the 'puzzle pieces' or research targeting multiple factors in orchard food webs to assess the functioning of the system as a whole (Fig. 2). This includes the effects of nutrients on trophic interactions and connectivity of the food web components, both above- and below -ground, over multiple spatial and temporal scales. Previous, specialized studies provide mixed and context-dependent results, which highlight a need for targeted long-term research in this area, particularly in perennial horticultural systems. For example, fertilizer additions have been found to induce both positive and negative effects on pests and pathogens but the mechanisms underlying nutrient stress signaling in the plant and the responses of pests and pathogens are not well understood (Fig. 2). These relationships are complex, with wide-ranging interactions in the ecosystem. Furthermore, much of the existing research on nutrient effects on food web dynamics compares conventional versus organic management systems or types of mulch and fertilizer applications rather than the specific mechanisms and drivers altering nutrient flows and ecosystem responses. To advance this area, we need to consolidate the 'puzzle pieces' from existing theory, and specialized food web components and mechanisms into a nutrient dynamics framework for orchard systems. By examining the drivers of nutrient flows, we will be able to identify any further gaps holding back our ability to predict outcomes of nutrient management changes.

6 Smart ways to improve nutrient practices

New tools are emerging to monitor plant nutrient dynamics and requirements as well as targeting fertilizer applications. These tools include advances in fertilizer application techniques, new methods to monitor plant and soil nutrients, modelling techniques to determine nutrient requirements and develop decision-support systems, and utilizing genetic variability to breed cultivars with improved plant nutrient use efficiency.

6.1 Adopting new application techniques

The majority of apple and kiwifruit orchards in New Zealand are largely rain-fed and have most nutrients applied through broadcast applications; however, recently more sustainable application methods are being adopted. Fertigation, where water and nutrients are supplied to match plant requirements, is one approach that has been used in other countries to improve the efficiency of both water and nutrient use while minimizing the detrimental effects of nutrient oversupply (Hagin and Lowengart 1996; Incrocci et al. 2017; Srivastava and Malhotra 2017). Fertigating can be used to supply precise measures of nutrients to better match plant demand at set time points as it allows a better distribution of nutrients in the plant root zone as well as the ability to maintain low nutrient concentrations in soil solution (Bar-Yosef 1999). Fertigation has therefore been associated with a large reduction in N losses from the soil in apples in a semiarid region of Canada where irrigation is required to maintain productivity (Neilsen and Neilsen, 2002). Early studies of fertigation in 'Hayward' kiwifruit production in New Zealand (Marsh and Stowell 1993) showed no beneficial effects on the yield or fruit quality, but the researchers did not investigate nutrient use efficiency. In apples, a comparison of broadcast and fertigation application has suggested that N application rates can be lowered by 75% using fertigation, but again, there were no effects on yield or fruit quality (Neilsen et al. 1999). Despite the benefit of fertigation, caution should be applied to its use in some contexts since it has also been associated with soil acidification, restricted root volume, and K deficiency using drip irrigation in some soil types or with strongly dwarfing rootstocks (Neilsen et al. 2000; Neilsen and Neilsen, 2005). Further improvements in nutrient use efficiency are possible using this technique in conjunction with new knowledge and new tools to measure various factors such as plant water use and nutrient uptake as well as soil water and soil nutrient status and health (Incrocci et al. 2017).

Nutrients can also be applied in dilute concentrations to plant canopies. This application method is advantageous in rainfed production systems where fertigation may not be possible. Foliar applications can be used to quickly supply nutrients to meet plant growth demands to correct nutrient

disorders and apply micronutrients, for example in apple trees (Kuresova et al. 2019). However, the quantity of nutrients that can be applied to plants via the foliage is much less than that which can be absorbed by roots and the uptake of nutrients through the stomata or cuticle can depend on the mineral nutrient, phenological stage, leaf age, leaf temperature, and stomatal conductance (Burkhardt 2010). Dong et al. (2005) compared the effects of foliar and soil N applications in apples and found that foliar N application reduced the risk of N leaching with no significant effects on tree N status, fruit yield, or quality. Applying 50% of fertilizer to the soil and 50% to apple leaves increased the N fertilizer use efficiency compared with that of N fertilizer applied only to the soil, as the leaves can absorb most of the fertilizer within a short time (Fernandez-Escobar et al. 2009). Foliar potassium nitrate (KNO_3) applications to 'Zesy002' kiwifruit vines in Bay of Plenty and Hawke's Bay, New Zealand, orchards significantly improved vine photosynthetic performance, nutrient status, and fruit characteristics such as size, firmness, soluble solid content, and fruit dry matter at harvest (Hashmatt et al. 2019). Spatial and temporal separation of soil-applied Ca and K fertilizer also improved nutrient uptake, photosynthetic performance, and at-harvest fruit quality of 'Zesy002' kiwifruit, while both soil-applied Ca and foliar-applied K increased kiwifruit vine N uptake Hashmatt (2020). Whilst fertilizing the soil and leaves or fertilizing the leaves alone has the potential to improve nutrient use efficiency care is required to ensure both the timing and frequency of applications are optimized. Shoots, especially young leaf tissue, can burn if the nutrient concentration is too high (Burkhardt 2010).

6.2 New measurement technologies

A wide range of newer technologies are being developed and utilized to monitor orchard nutrient status and tailor fertilizer applications to achieve sustainable outcomes. Sap nutrient analysis has been widely used in vegetable crops and has been used to predict N in apple leaves (Almeida et al. 2020). Imaging technologies are also being developed and used in fruit crops such as nondestructive leaf chlorophyll meters, which have been successfully used to assess leaf N status in a range of crops including apples (Lee et al. 2019). Hyperspectral imaging techniques, capable of estimating measures such as leaf chlorophyll, N, and water content (Lu et al. 2020) have been used at both a leaf and a canopy level in apple crops (Ye et al. 2020). These techniques are also being used to remotely monitor the spatial and temporal variability of crops (Lu et al. 2020). For tomatoes, Sun et al. (2019) have developed multispectral three-dimensional imaging for determining N, P, and K of glasshouse tomato plants, which is more robust in determining nutrient content in contrast to two-dimensional or single-point measurements. However, they report that plant movement or shaking of soft plant stems prevented accurate three-dimensional registration. Another important consideration for the potential use of spectral techniques to determine plant mineral element status is the inability of these techniques to penetrate the object and they are unsuitable for the identification of nutrient levels for tissues with low homogeneity. Imaging technologies lend themselves to the implementation of precision agriculture and should enable more precise measures of individual plant nutrient status during the growing season.

To improve fertilization practices, an understanding of the ability of soils to supply nutrients is also required. Recent technological advances have provided new opportunities to understand how variations in soil type, temperature, and moisture affect their ability to supply nutrients. Electromagnetic induction mapping (EM) allows a rapid assessment of differences in soil properties (such as texture and moisture) to be performed (Doolittle and Brevik 2014). Rapid analysis of soil solution extracts using photometers or ion-specific sensors or measuring soil N directly using NIR reflectance, allows regular monitoring of vegetable crops (Incrocci et al. 2017) but has not been widely used in perennial fruit crops. Targeted plant and soil sampling are still required to validate data from new measurement methods.

To take maximum advantage of new knowledge and technologies to improve perennial fruit crop nutrient management, models of key plant and soil processes need to be developed and used to form decision-support systems. These tools are commonly used in arable and vegetable crops (Incrocci et al. 2017). Models have been developed, for example, to examine orchard fertilizer practices (Nesme et al. 2005) and to model the N content of apple trees determined from hyperspectral imaging (Ye et al. 2020) but there are no equivalent studies in kiwifruit. Many processes, including nutrient cycling and balances and food web dynamics, have yet to be modelled in apple and kiwifruit orchard systems and used to formulate effective decision-support tools.

6.3 New rootstock and scion genetics

Variation in plant scion and rootstock genetics and interactions between them provide an important route for improving nutrient use efficiency in orchard ecosystems. Breeding of scions and rootstocks for perennial fruit crops has traditionally focused on improving yield, fruit quality, and pest and disease resistance, as well as reducing plant vigor and increasing tolerance to environmental conditions. Rootstocks are widely used in apple orchards and benefits can include these factors as well as tolerance to poor soil conditions, avoidance of nutrient disorders like bitter pit, and more recently, enhanced leaf nutrient uptake (Amiri et al. 2014; Neilsen et al. 2018; Valverdi and Kalcsits 2021). Advances in understanding have allowed progress in customising apple rootstock nutrient uptake capabilities to meet scion requirements in specific

environments (Fazio et al. 2013; Reig et al. 2018). New understanding of the effects of symbiotic relationships between apple rootstocks and mycorrhiza on growth, gas exchange, nutrient uptake, and efficiency is also important (Dalla Costa et al. 2021). However, the mechanisms involved in nutrient acquisition and the role of rootstock and scion and rootstock genetics needs to be fully explored in apple and other fruit crops (Kalcsits et al. 2020). In kiwifruit orchards, the benefits of rootstocks are still being explored, with the majority of orchards being planted on seedling rootstocks or on their own roots. New understanding, together with advances in genotyping methods that take account of the many factors involved, will lead to the development of new scion and rootstock cultivars with greater nutrient use efficiency for apples and kiwifruit.

7 Conclusions and perspectives

Our review has identified significant knowledge gaps limiting our understanding of nutrient dynamics in modern perennial horticulture systems. We took a novel, system-level approach to examine nutrient interactions in orchards to develop a research roadmap for optimizing nutrient management in apples and kiwifruit. The major knowledge gaps identified (Fig. 2) provide challenges for reducing nutrient inputs in orchard ecosystems without negatively affecting fruit quantity and quality. Key research priorities include the following: (1) understanding the relationship between carbon and nutrients, and nutrient demand, in modern fruit cultivars and growing systems, (2) quantifying the nutrient balance for perennial horticultural crops, considering all inputs and outputs, and (3) synthesizing research targeting multiple factors in orchard food webs, considering both above- and below-ground nutrient flows. New research is needed to address these knowledge gaps to reduce the adverse effects of nutrients and greenhouse gas emissions on the environment.

While there is a great opportunity for biophysical and social studies to start addressing these priorities, one of the most significant challenges for perennial horticulture nutrient management research is the long-term time scale required to understand nutrient dynamics in a perennial horticultural crop. This is due to nutrient storage and remobilization in perennial tissue over long temporal scales, and the time required to produce a fruit crop from plant establishment. Targeted experiments will require the use of isotopic tracer methodology to unravel nutrient movement through the agroecosystem over multiple seasons. Non-destructive measurement techniques to monitor plant and soil nutrient status offer new means to collect real-time data, which can be used to make better predictions of plant nutrient demands to guide nutrient applications. However, links to new imaging and sensing technologies need to be verified with robust destructive measurements. Finally, we need research encompassing the complete orchard system to better predict and mitigate the environmental impacts of nutrient inputs on the whole agroecosystem and its supported food webs.

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