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Dynamic Source-Sink Regulation and Carbon Allocation in Fruit Crops: Implications for Yield, Quality, and Climate Resilience

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Abstract— *Carbon allocation and source-sink interactions are fundamental determinants of yield, fruit quality, and climate resilience in perennial fruit crops. Unlike annual species, fruit crops must continuously distribute assimilates among reproductive, vegetative, and storage sinks, balancing current production with future growth. Although photosynthetic carbon supply has traditionally been regarded as the primary driver of productivity, increasing evidence shows that sink demand actively regulates source activity through metabolic and signalling feedback, making crop performance dependent on the coordinated interaction of source capacity, sink strength, phloem transport, and non-structural carbohydrate reserves. This review synthesizes current physiological, biochemical, and modelling knowledge to develop an integrated framework for understanding carbon allocation in major fruit crops, including apple, grapevine, citrus, peach, and mango. It examines the roles of carbohydrate reserves, sink activity, and phloem transport in regulating fruit growth, quality, and seasonal carry-over effects, while highlighting the impacts of drought, heat stress, elevated atmospheric CO_2, and nutrient limitations on source-sink coordination. Emerging approaches for analysing carbon dynamics and key research priorities are also discussed. Optimizing sink activity and reserve dynamics, together with climate-smart orchard management, is essential for sustaining fruit productivity, quality, and resilience under changing climatic conditions.*

Keywords— Carbon allocation; source-sink; sink strength; photoassimilates; non-structural carbohydrates; climate resilience.

I. INTRODUCTION

The productivity and sustainability of perennial fruit crops depend not only on carbon assimilation but also on the efficient allocation of photoassimilates among vegetative, reproductive, and storage sinks. Unlike annual crops, fruit trees and vines must simultaneously support current-season fruit development, maintain perennial structures, and accumulate reserves for future growth. Consequently, carbon allocation is a major determinant of yield stability, fruit quality, and long-term orchard performance (Pallas *et al.*, 2018; White *et al.*, 2016).

Carbon allocation comprises the transport, distribution, storage, remobilization, and utilization of assimilated carbon, whereas carbon partitioning describes its distribution among competing sinks during development (Marcelis & Heuvelink, 2007). Source capacity denotes the ability of photosynthetically active organs to produce and export assimilates, while sink strength reflects the capacity of developing organs to attract and utilize them according to their size and metabolic activity (Marcelis, 1996). In perennial fruit crops, non-structural carbohydrate (NSC) reserves stored in roots, trunks, and branches buffer temporal imbalances between carbon supply and demand and sustain growth during periods of limited photosynthesis (Martínez-Vilalta *et al.*, 2016).

Although traditional models emphasize photosynthetic carbon supply as the principal determinant of productivity, increasing evidence shows that sink demand actively regulates source activity through metabolic feedback and signalling pathways controlling photosynthesis, assimilate export, and carbon allocation (Paul & Foyer, 2001; Osorio *et al.*, 2014). Carbon allocation is closely linked with nitrogen metabolism, as changes in carbon metabolism and the carbon-to-nitrogen (C/N) ratio accompany physiological disorders in mango, emphasizing coordinated carbon-nitrogen regulation of source-sink balance (Khan & Zaidi, 2000). In addition, alternate bearing, seasonal reserve remobilization, and rootstock-scion interactions further influence carbon partitioning, water relations, productivity, and fruit quality (Martínez-Vilalta *et al.*, 2016; Tworkoski & Fazio, 2015).

At the molecular level, source-sink coordination is regulated by sugar signalling pathways, hormonal networks, and transport processes. Trehalose-6-phosphate (T6P), sucrose non-fermenting-1-related protein kinase 1 (SnRK1), and target of rapamycin (TOR) integrate carbon status with developmental and environmental signals to regulate carbohydrate metabolism and sink activity (Figueroa & Lunn, 2016; Li *et al.*, 2022).

Climate change increasingly exposes the limitations of supply-driven models. Elevated atmospheric CO_2 often enhances photosynthesis without proportional yield gains because of sink limitations and nutrient constraints, whereas drought and heat stress frequently impair sink function before substantially reducing photosynthesis (Ainsworth & Long, 2021; Lakso *et al.*, 2001; Sukhvibul *et al.*, 2005). Therefore, understanding source-sink regulation and carbon allocation is essential for improving fruit yield, quality, and climate resilience.

While several excellent reviews have addressed aspects of source-sink relations in crops (Paul & Foyer, 2001; Marcelis, 1996; White *et al.*, 2016; Pallas *et al.*, 2018), a comprehensive synthesis that integrates molecular mechanisms, whole-plant physiology, climate interactions, and practical management strategies across major fruit crops is lacking. This review addresses this gap by providing a unified framework that connects molecular regulation (T6P, SnRK1, TOR signalling) with whole-plant carbon dynamics and orchard-level management, while specifically evaluating the implications of multiple climate stressors. The review also incorporates emerging tools—including isotopic tracing, high-throughput phenotyping, and digital twin modelling—that are transforming our ability to predict and manage carbon allocation in perennial systems. This synthesis is intended to serve as a resource for researchers, breeders, and orchard managers seeking to optimize carbon-use efficiency and climate resilience in fruit production systems.

II. REVIEW METHODOLOGY

A comprehensive literature review was undertaken to synthesize current knowledge on source-sink regulation and carbon allocation in fruit crops. Relevant peer-reviewed research articles, review papers, books, book chapters, conference proceedings, and technical reports published between 1980 and 2025 were collected from major scientific databases, including Web of Science, Scopus, ScienceDirect, SpringerLink, Wiley Online Library, Google Scholar, and ResearchGate. Search terms included combinations of "source-sink," "carbon allocation," "fruit crops," "sink strength," "non-structural carbohydrates," "climate change," and specific crop names. The retrieved literature was critically evaluated for scientific quality, relevance, and contribution to the understanding of carbon dynamics in horticultural systems. Classical studies establishing the theoretical framework of source-sink relationships were integrated with recent advances in molecular biology, physiology, phenomics, and climate change research.

III. CONCEPTUAL FRAMEWORK OF SOURCE-SINK DYNAMICS

Carbon allocation in fruit crops is governed by interactions among carbon acquisition, transport, utilization, storage, and remobilization. These processes are particularly complex in perennial systems, where assimilates must be distributed among multiple competing sinks that vary in demand across developmental stages and seasons (Pawar *et al.*, 2019). Understanding source-sink dynamics therefore requires consideration of both the temporal and spatial dimensions of carbon movement.

3.1 Defining Carbon Allocation and Carbon Partitioning

Carbon allocation encompasses the transport, distribution, storage, remobilization, and utilization of assimilated carbon throughout the plant, whereas carbon partitioning refers to the proportional distribution of assimilates among competing organs at a given developmental stage (Marcelis & Heuvelink, 2007). In perennial fruit crops, carbon allocation extends beyond a single growing season because stored carbohydrates support future growth, flowering, and fruiting, requiring evaluation across seasonal and interannual timescales (Martínez-Vilalta *et al.*, 2016).

3.2 Source Capacity and Sink Strength

Source organs export assimilates in excess of their own requirements, whereas sink organs import carbon for growth, storage, and maintenance (Paul & Foyer, 2001). Mature leaves are the primary sources, while developing fruits, shoot apices, roots, and storage tissues function as major sinks (Marcelis, 1996). Source capacity is influenced by photosynthetic activity, canopy structure, and environmental conditions, whereas sink strength is determined by sink size and metabolic activity (Marcelis, 1996; White *et al.*, 2016). During periods of rapid growth, fruits become dominant sinks that strongly influence carbon distribution, yield, and quality (Osorio *et al.*, 2014).

3.3 Phloem Transport and Source-Sink Coordination

Photoassimilates are transported through the phloem via hydrostatic pressure gradients generated by sucrose loading and unloading, consistent with the pressure-flow hypothesis (Knoblauch & Oparka, 2012). Carbon transport is regulated by source supply, sink demand, and carbohydrate-mediated feedback on transport efficiency (Paul & Foyer, 2001). Environmentally driven nutrient effects on photosynthate partitioning and delayed senescence further demonstrate the dynamic regulation of source-sink relationships in horticultural crops (Ghazannfar Ghani *et al.*, 2019). The coordinated movement of assimilates from source leaves to vegetative, reproductive, and storage sinks is illustrated in Figure 1.

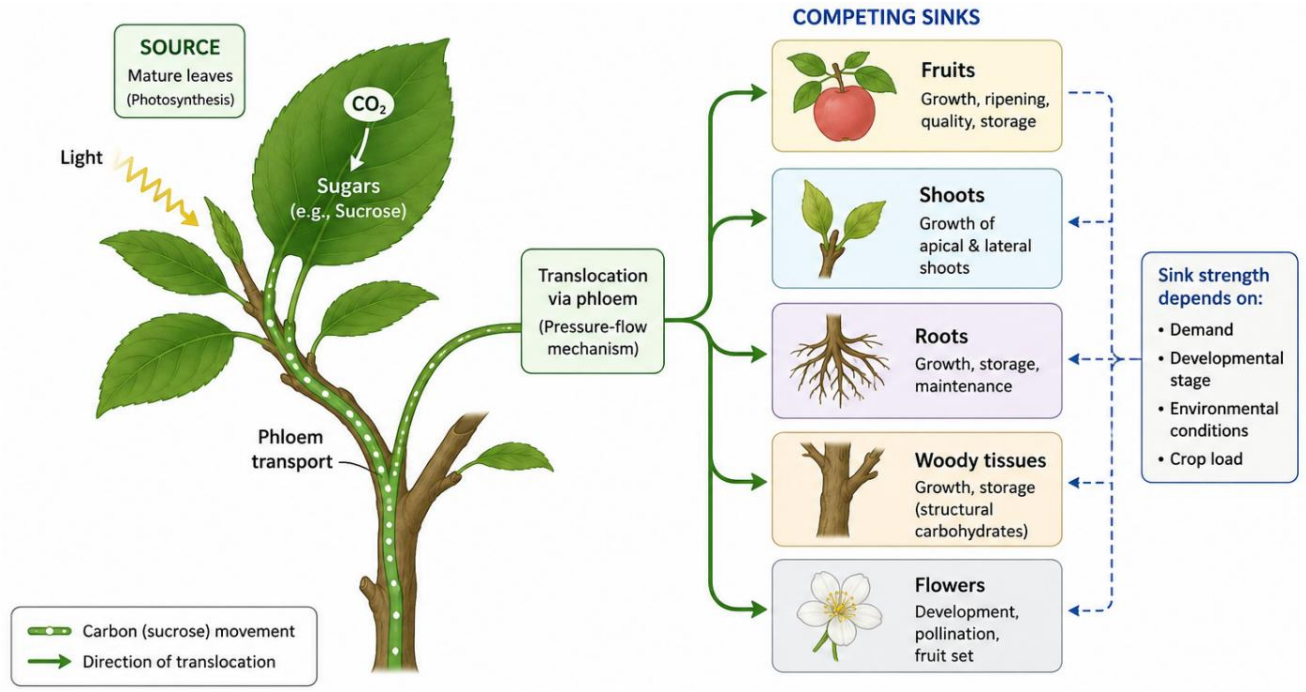

FIGURE 1: Simplified framework of carbon movement from source leaves to competing sinks in fruit crops. Photosynthates produced in source leaves are transported via phloem and partitioned among competing sinks.

Sugar signalling pathways, including trehalose-6-phosphate (T6P), sucrose non-fermenting-1-related protein kinase 1 (SnRK1), and target of rapamycin (TOR), integrate carbon availability with sink activity and growth (Figueroa & Lunn, 2016; Li *et al.*, 2022). Hormonal networks further regulate sink establishment and stress responses (McAtee *et al.*, 2013).

3.4 Reserve Buffering and Temporal Dynamics

Non-structural carbohydrate (NSC) reserves stored in perennial organs buffer temporal mismatches between carbon supply and demand. These reserves support early-season growth, flowering, and fruit set before canopy photosynthesis reaches full capacity (Loescher *et al.*, 1990). Reserve dynamics are influenced by crop load, phenology, and environmental conditions, with inadequate replenishment contributing to alternate bearing and reduced resilience (Pawar *et al.*, 2019; Martínez-Vilalta *et al.*, 2016).

3.5 A Dynamic Systems Perspective

Productivity in fruit crops is determined by the dynamic interaction among source capacity, sink strength, phloem transport, and reserve buffering rather than by carbon assimilation alone. Sink limitations can constrain photosynthetic responses, resulting in carbohydrate accumulation without proportional increases in growth or yield (Paul & Foyer, 2001; Ainsworth & Long, 2021). Therefore, source-sink dynamics should be viewed as a feedback-regulated system underpinning fruit yield, quality, and climate resilience.

IV. SOURCE CAPACITY: DETERMINANTS AND REGULATION

Source capacity is the ability of photosynthetically active tissues to assimilate and export carbon beyond their own metabolic requirements. In fruit crops, mature leaves are the principal source organs supporting vegetative growth, fruit development, respiration, and reserve accumulation (Marcelis, 1996). Source capacity is influenced by leaf characteristics, canopy architecture, environmental conditions, phenological stage, and sink demand.

4.1 Leaf-Level Determinants of Source Capacity

Photosynthetic carbon assimilation is the primary determinant of source capacity. Net photosynthesis depends on stomatal conductance, chlorophyll content, electron transport efficiency, and Rubisco activity. Developing leaves transition from sinks to sources during maturation (Turgeon, 2010). Nutrient availability, particularly nitrogen, magnesium, potassium, and iron, strongly influences photosynthetic performance and assimilate export (Marschner, 2012). Leaf anatomical traits, including specific leaf area and stomatal density, further affect source efficiency (White *et al.*, 2016).

4.2 Canopy Architecture and Light Interception

Whole-plant source capacity depends on the quantity and distribution of photosynthetically active leaf area. Canopy architecture influences light interception and radiation use efficiency, with excessive canopy density reducing photosynthesis in interior leaves (Palmer *et al.*, 1992). Consequently, pruning, training systems, and planting density play key roles in optimizing carbon acquisition and fruit growth (Keller, 2020).

4.3 Environmental Regulation of Source Capacity

Light, temperature, water availability, and nutrient status strongly regulate source capacity. Drought reduces photosynthesis through stomatal closure and impaired leaf water status, while heat stress decreases photosynthetic efficiency by increasing photorespiration and damaging the photosynthetic machinery (Chaves *et al.*, 2010; Urban *et al.*, 2017). Elevated atmospheric CO_2 generally enhances photosynthesis in C_3 fruit crops, although its benefits are often constrained by sink limitations and nutrient availability (Ainsworth & Long, 2021). Likewise, nutrient availability influences assimilate production and partitioning, with foliar nutrient application improving photosynthate distribution and delaying senescence under contrasting environmental conditions (Ghazannfar Ghani *et al.*, 2019).

4.4 Sink Feedback Regulation of Source Activity

Source activity is closely regulated by sink demand. Reduced sink capacity promotes carbohydrate accumulation in leaves, suppressing photosynthesis and assimilate export through sugar-signalling pathways involving trehalose-6-phosphate (T6P), sucrose non-fermenting-1-related protein kinase 1 (SnRK1), and target of rapamycin (TOR) (Paul & Foyer, 2001; Figueroa & Lunn, 2016; Li *et al.*, 2022). Altered carbon metabolism and the carbon-to-nitrogen (C/N) balance under physiological disorders in mango further highlight the close coordination between carbon and nitrogen metabolism in source-sink regulation (Khan & Zaidi, 2000). Conversely, strong reproductive demand can stimulate photosynthesis but may induce source limitation when fruit demand exceeds canopy supply.

4.5 Temporal Dynamics of Source Capacity in Perennial Fruit Crops

Source capacity changes throughout the growing season. Early growth relies largely on remobilized carbohydrate reserves because newly emerged leaves are not fully photosynthetically active (Loescher *et al.*, 1990). As the canopy develops, current photosynthesis becomes the primary carbon source for fruit growth and reserve replenishment, whereas later assimilate allocation shifts to perennial storage organs to support subsequent growth and reproduction (Pawar *et al.*, 2019). Sustained source activity through delayed senescence and efficient assimilate partitioning is therefore essential for maintaining carbon supply during later developmental stages (Ghazannfar Ghani *et al.*, 2019).

V. SINK STRENGTH AND SINK ACTIVITY IN FRUIT CROPS

Sink strength is a major determinant of carbon allocation in fruit crops because it governs the ability of organs to attract and utilize photoassimilates. In perennial species, fruits, shoots, roots, cambial tissues, and storage organs compete for limited carbon resources throughout the growing season, influencing yield, fruit quality, and long-term productivity.

5.1 Defining Sink Strength and Sink Activity

Sink strength is defined as the capacity of an organ to import assimilates and is determined by the product of sink size and sink activity (Marcelis, 1996). Sink size refers to the physical dimensions or biomass of a sink, whereas sink activity reflects its physiological capacity to unload, metabolize, and utilize assimilates (Ho, 1988). Developing fruits are typically the dominant sinks because of their high carbon demand during growth and storage compound accumulation (Osorio *et al.*, 2014).

5.2 Developmental Dynamics of Fruit Sink Strength

Fruit sink strength varies throughout development. Early cell division determines sink size, while subsequent cell expansion and storage compound accumulation enhance sink activity (Marcelis, 1996). Consequently, sink demand differs among developmental stages and fruit species. Crop load strongly regulates sink competition; excessive fruit numbers reduce assimilate availability per fruit, whereas fruit thinning enhances sink strength, fruit size, and sugar accumulation (Lakso & Corelli Grappadelli, 1992). Similar responses have been demonstrated in high-density apple orchards, where fruitlet thinning improved fruit production and quality by reducing sink competition (Mehvish Bashir *et al.*, 2023).

5.3 Physiological and Molecular Regulation of Sink Activity

Sink activity depends on the efficiency of phloem unloading and carbohydrate metabolism (Patrick, 1997). Enzymes such as invertases and sucrose synthase maintain concentration gradients that facilitate assimilate import and utilization (Ruan, 2014). In addition, sugar-signalling pathways involving trehalose-6-phosphate (T6P), sucrose non-fermenting-1-related protein kinase 1 (SnRK1), and target of rapamycin (TOR) integrate carbon availability with sink development and growth (Figueroa & Lunn, 2016; Li *et al.*, 2022). Hormonal networks, including auxins, cytokinins, gibberellins, and abscisic acid, further regulate sink establishment and assimilate unloading (McAtee *et al.*, 2013).

5.4 Factors Influencing Sink Strength and Fruit Quality

Sink strength is influenced by genotype, developmental stage, rootstock-scion interactions, and environmental conditions (Marcelis, 1996; Tworkoski & Fazio, 2015). Drought, heat stress, and nutrient deficiencies can reduce cell expansion, assimilate transport, and carbohydrate utilization, thereby limiting fruit growth and sink demand (Marschner, 2012; Sukhvibul *et al.*, 2005).

Fruit yield and quality depend not only on carbon supply but also on the ability of fruits to compete for assimilates. Strong sink activity promotes the accumulation of sugars, organic acids, pigments, and secondary metabolites, whereas excessive crop loads reduce fruit size, soluble solids concentration, and postharvest quality. Because perennial fruit crops must also replenish carbohydrate reserves, balancing current fruit demand with reserve accumulation is essential for sustaining productivity across seasons (Paul & Foyer, 2001; Pawar *et al.*, 2019).

5.5 Species-Specific Differences in Sink Dynamics

It is important to acknowledge that sink dynamics differ substantially among fruit crop species. Temperate deciduous species (e.g., apple, peach) exhibit strong seasonal reserve remobilization, with carbohydrate reserves playing a critical role in early spring growth. Evergreen subtropical species (e.g., citrus, mango) maintain photosynthetic activity year-round and may rely less on reserve mobilization. Additionally, species differ in their primary transport carbohydrates: most fruit crops transport sucrose, but species in the Rosaceae family (apple, pear) transport significant amounts of sorbitol in addition to sucrose, with implications for phloem loading and unloading mechanisms. These species-specific differences should be considered when applying general principles to particular crops.

VI. PHLOEM TRANSPORT AND CARBON PARTITIONING MECHANISMS

Efficient transport and partitioning of photoassimilates are central to source-sink coordination in fruit crops. Carbon fixed through photosynthesis must be translocated from source leaves to fruits, vegetative tissues, roots, and storage organs through

the phloem network. The regulation of this process determines fruit growth, quality, reserve accumulation, and long-term productivity (Patrick, 1997; Pawar *et al.*, 2019).

6.1 Mechanisms of Long-Distance Carbon Transport

Sucrose is the principal transport carbohydrate in most fruit crops, although sugar alcohols such as sorbitol in apple and pear also contribute to long-distance translocation. According to the pressure-flow hypothesis, active phloem loading at source tissues generates hydrostatic pressure gradients that drive assimilate movement towards sinks, where sugars are unloaded and utilized (Knoblauch & Oparka, 2012). Phloem transport is dynamic and responds to source activity, sink demand, and environmental conditions (De Schepper *et al.*, 2013).

6.2 Phloem Loading and Unloading Pathways

Phloem loading and unloading occur through symplastic or apoplastic pathways depending on species and developmental stage (Turgeon, 2010). Sucrose transporters (SUTs) and SWEET proteins regulate membrane transport and influence carbon export efficiency and sink strength (Chen *et al.*, 2012). In many fruit species, unloading shifts from symplastic to apoplastic pathways during fruit maturation, facilitating sugar accumulation and enhanced sink activity (Ruan & Patrick, 1995).

6.3 Carbon Partitioning among Competing Sinks

Carbon partitioning describes the distribution of assimilates among fruits, shoots, roots, and storage organs according to their relative sink strength (Marcelis & Heuvelink, 2007). Allocation patterns vary with phenological stage and crop load. Early growth depends largely on stored carbohydrates, whereas fruits become dominant sinks during rapid growth phases (Lakso & Corelli Grappadelli, 1992). Following harvest, carbon allocation shifts towards replenishment of non-structural carbohydrate reserves in perennial tissues (Martínez-Vilalta *et al.*, 2016).

6.4 Regulation of Carbon Partitioning

Carbon partitioning is regulated by source capacity, sink strength, vascular connectivity, and environmental conditions (Patrick, 1997). Environmental and nutritional factors modify assimilate distribution, as evidenced by altered photosynthate partitioning under different foliar nutrient regimes in horticultural crops (Ghazannfar Ghani *et al.*, 2019). Sugar-signalling pathways involving trehalose-6-phosphate (T6P), sucrose non-fermenting-1-related protein kinase 1 (SnRK1), and target of rapamycin (TOR), together with hormonal signals and rootstock-scion interactions, further coordinate carbon allocation and sink activity (Figueroa & Lunn, 2016; Li *et al.*, 2022; McAtee *et al.*, 2013; Tworkoski & Fazio, 2015).

6.5 Environmental Effects on Phloem Transport and Partitioning

Environmental stresses can disrupt phloem transport and alter carbon allocation. Drought reduces phloem turgor and assimilate translocation, while heat stress impairs membrane integrity and transport efficiency (Sevanto, 2014; De Schepper *et al.*, 2013). Although elevated atmospheric CO_2 generally enhances photosynthesis, its benefits may be limited by sink demand and phloem transport capacity (Ainsworth & Long, 2021). Nutrient deficiencies, particularly of potassium and boron, can further restrict phloem function and fruit development (Marschner, 2012).

Overall, phloem transport and carbon partitioning determine the efficiency of assimilate distribution among competing sinks and underpin fruit yield, quality, reserve accumulation, and climate resilience in perennial fruit crops.

VII. NON-STRUCTURAL CARBOHYDRATE RESERVES AND CARRY-OVER EFFECTS

Non-structural carbohydrates (NSCs) are a key component of carbon allocation in perennial fruit crops, buffering temporal imbalances between carbon supply and demand. Unlike annual species, fruit trees and vines depend on stored carbohydrate reserves to sustain growth, reproduction, and survival across multiple years, linking current carbon status with future productivity (Martínez-Vilalta *et al.*, 2016).

7.1 Nature and Functions of Non-Structural Carbohydrate Reserves

NSCs comprise soluble sugars, including sucrose, glucose, fructose, sorbitol, and mannitol, together with starch reserves stored in roots, trunks, branches, and woody tissues (Loescher *et al.*, 1990). These reserves accumulate during periods of carbon surplus and are remobilized when demand exceeds current photosynthetic supply. Beyond carbon storage, NSCs support respiration, osmotic regulation, and stress tolerance, particularly during early-season growth when developing shoots, flowers, and fruits rely heavily on stored reserves (Hartmann & Trumbore, 2016; Pawar *et al.*, 2019).

7.2 Seasonal Dynamics and Carry-Over Effects

NSC accumulation and remobilization follow seasonal phenological cycles. Carbohydrate reserves are replenished during post-harvest and dormancy and mobilized at bud break, flowering, and early fruit development before canopy photosynthesis is fully established (Loescher *et al.*, 1990; Martínez-Vilalta *et al.*, 2016). During fruit development, progressive accumulation of total, reducing, and non-reducing sugars reflects dynamic photoassimilate allocation to developing sinks, as demonstrated in apple (Dar *et al.*, 2021). Crop load strongly influences reserve dynamics, as high reproductive demand limits reserve replenishment.

Reserve mobilization creates carry-over effects by linking carbon allocation across successive seasons. Reserve depletion during heavy fruiting reduces subsequent flowering, fruit set, and vegetative growth, contributing to alternate bearing, whereas adequate reserve accumulation enhances productivity and reproductive performance in the following season (Goldschmidt, 2013; Pawar *et al.*, 2019).

7.3 Environmental Regulation of Reserve Dynamics

Environmental conditions strongly influence NSC accumulation and utilization. Drought, heat stress, nutrient deficiencies, and defoliation reduce carbon assimilation and limit reserve replenishment (Hartmann & Trumbore, 2016). Prolonged stress can deplete reserves as maintenance respiration continues despite reduced photosynthesis (Sevanto *et al*., 2014). Although elevated atmospheric CO_2 may enhance carbon assimilation, reserve storage can remain constrained by sink limitations and nutrient availability (Ainsworth & Long, 2021).

Maintaining adequate NSC reserves is therefore essential for sustaining yield, fruit quality, and climate resilience in perennial fruit crops (Martínez-Vilalta *et al.*, 2016).

7.4 Implications for Orchard Management

Orchard management practices that influence source-sink balance directly affect non-structural carbohydrate reserve dynamics and long-term productivity. Crop load management, pruning, irrigation, nutrient supply, and harvest timing determine reserve accumulation and subsequent reproductive performance (Lakso & Corelli Grappadelli, 1992). Practices such as fruit thinning and maintaining adequate post-harvest leaf area enhance reserve replenishment, improve return bloom, and reduce alternate bearing (Goldschmidt, 2013; Pawar *et al.*, 2019). Therefore, sustainable orchard management should balance current fruit production with adequate reserve restoration to ensure productivity and resilience across seasons.

VIII. CARBON ALLOCATION AND FRUIT QUALITY

Fruit quality is determined not only by genetics and environmental conditions but also by the efficiency and timing of carbon allocation to developing fruits. The quantity and distribution of assimilates influence fruit size, sweetness, acidity, colour, firmness, aroma, nutritional value, and post-harvest performance (Kader, 2008). Therefore, fruit quality is an outcome of dynamic source-sink interactions rather than total carbon assimilation alone.

8.1 Carbon Supply and Fruit Growth

Fruit size and dry matter accumulation depend on carbon availability during key developmental stages. Adequate assimilate supply during early development supports cell division and establishes potential fruit size, whereas sustained carbon availability during later stages promotes cell expansion and biomass accumulation (Marcelis, 1996). Crop load strongly influences carbon allocation; excessive fruit numbers reduce assimilate availability per fruit, while fruit thinning improves fruit size, uniformity, and quality (Lakso & Corelli Grappadelli, 1992; Pawar *et al.*, 2019).

8.2 Carbon Allocation and Sugar-Acid Balance

The balance between sugars and organic acids is a major determinant of fruit flavour and consumer acceptance. Imported assimilates are converted into species-specific sugars and organic acids through coordinated metabolic processes, and the progressive accumulation of total, reducing, and non-reducing sugars during apple fruit development further demonstrates the close link between assimilate partitioning and fruit quality (Ruan, 2014; Dar *et al.*, 2021). Conversely, excessive crop load or environmental stress can reduce carbon availability, lowering soluble solids concentration and impairing flavour quality (Keller, 2020).

8.3 Carbon Allocation and Secondary Metabolites

Carbon availability influences the synthesis of secondary metabolites, including anthocyanins, carotenoids, phenolics, and volatile compounds that determine fruit colour, aroma, nutritional value, and health-promoting properties (Stamp, 2003). Sugar-signalling pathways further regulate the accumulation of these compounds during fruit development and ripening (Figueroa & Lunn, 2016).

8.4 Carbon Allocation, Texture, and Post-harvest Quality

Carbon status influences fruit texture, dry matter accumulation, and aroma by regulating cell wall synthesis and volatile production (Kader, 2008). Higher dry matter and antioxidant contents are associated with improved flavour, storage performance, and resistance to physiological disorders (Palmer *et al.*, 2013). Likewise, appropriate harvest timing, preharvest calcium application, and crop-load management through fruitlet thinning enhance carbon availability and fruit quality while reducing physiological disorders such as watercore and sink competition (Khan *et al.*, 2023; Mehvish Bashir *et al.*, 2023).

8.5 Environmental Modulation of Carbon-Quality Relationships

Environmental conditions alter carbon allocation by affecting both source activity and sink function. Drought and heat stress can reduce fruit size and impair carbohydrate metabolism, pigment synthesis, and flavour development (Chaves *et al.*, 2010; Sugiura *et al.*, 2013). Although elevated atmospheric CO_2 often enhances photosynthesis, improvements in fruit quality depend on the capacity of fruits to utilize and store additional assimilates (Ainsworth & Long, 2021).

Optimizing carbon allocation through crop load management, canopy architecture, irrigation, and nutrient management is therefore essential for enhancing fruit quality and maintaining productivity under changing climatic conditions.

IX. SOURCE-SINK DYNAMICS UNDER MULTIPLE CLIMATE STRESSORS

Climate change is exposing fruit crops to increasingly frequent droughts, heat waves, elevated atmospheric CO_2, erratic precipitation, and extreme weather events that often occur simultaneously. These interacting stressors disrupt source capacity, sink strength, phloem transport, and reserve dynamics, thereby affecting yield stability, fruit quality, and long-term resilience (IPCC, 2023).

9.1 Drought-Induced Disruptions in Source-Sink Coordination

Drought alters carbon allocation through both source- and sink-related mechanisms. Reduced soil moisture limits stomatal conductance and photosynthesis, while sink processes such as cell expansion, phloem unloading, and assimilate utilization are often more sensitive to water deficits than carbon assimilation itself (Chaves *et al.*, 2010; Hsiao & Xu, 2000). Reduced sink activity leads to carbohydrate accumulation in leaves, feedback inhibition of photosynthesis, and impaired fruit growth and reserve replenishment (Paul & Foyer, 2001). Drought also restricts phloem transport by reducing hydrostatic pressure gradients, increasing the risk of carbon starvation (Sevanto, 2014).

9.2 Heat Stress and Phenological Mismatches

Heat stress increases respiratory carbon losses and reduces photosynthetic efficiency through enhanced photorespiration and damage to photosynthetic machinery (Urban *et al.*, 2017). Reproductive processes, including flowering and fruit set, are particularly sensitive to high temperatures, resulting in reduced sink strength and fruit retention (Sukhvibul *et al.*, 2005). Climate warming can also advance phenological development, increasing dependence on stored carbohydrates and heightening the risk of source-sink mismatches (Pawar *et al.*, 2019).

9.3 Elevated CO_2 and Sink Limitation

Elevated atmospheric CO_2 generally enhances photosynthesis in C_3 fruit crops; however, productivity gains are often constrained by sink limitations (Ainsworth & Long, 2021). When sink demand does not increase proportionally, carbohydrates accumulate in source tissues, leading to photosynthetic acclimation and reduced carbon-use efficiency (Paul & Foyer, 2001). Nutrient constraints may further limit the utilization of additional assimilates (Terrer *et al.*, 2020).

9.4 Combined Stress Effects and Carbon Allocation Trade-Offs

Combined drought and heat stress disrupt source-sink coordination more severely than individual stressors because high temperatures increase respiratory demand while drought restricts carbon acquisition and transport (Urban *et al.*, 2017). Under multiple stresses, plants often prioritize carbon allocation to survival functions, including osmotic adjustment and root growth,

at the expense of fruit development and reserve accumulation (Chaves *et al.*, 2010). Extreme events such as late frosts, hailstorms, and unseasonal rainfall further disturb source-sink balance by damaging photosynthetic or reproductive tissues. The interactive effects of major climate stressors on source capacity, sink strength, phloem transport, carbon partitioning, and fruit crop performance are summarized in Figure 2.

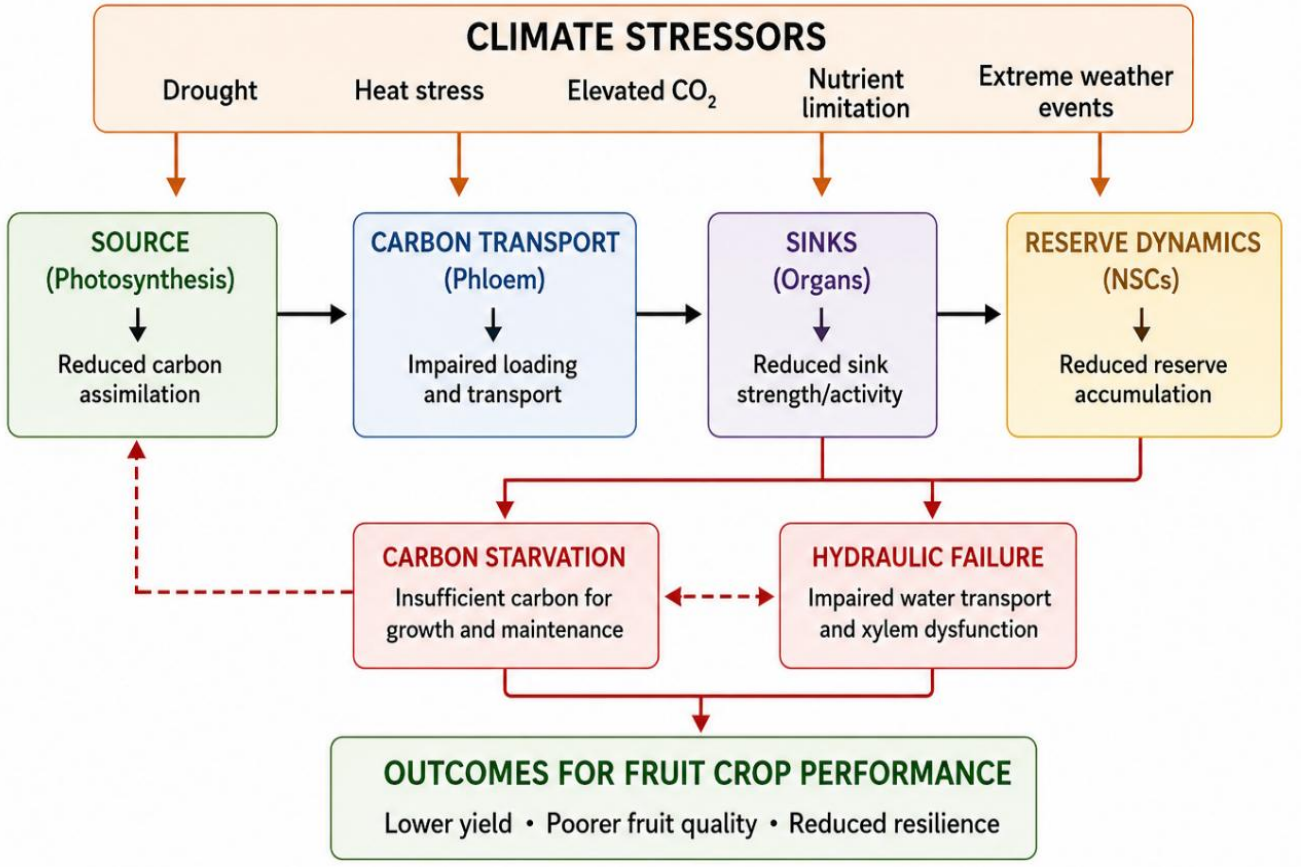

FIGURE 2: Influence of climate stressors on source-sink dynamics, carbon allocation, and fruit crop performance.

9.5 Carbon Starvation, Hydraulic Failure, and Resilience

Carbon starvation, resulting from depletion of non-structural carbohydrate reserves, and hydraulic failure, caused by impaired water transport, are key mechanisms underlying plant responses to prolonged stress (Sevanto *et al.*, 2014). These processes are closely interconnected because disruptions in phloem transport can simultaneously limit carbon delivery and impair hydraulic function (Hartmann & Trumbore, 2016). Therefore, maintaining source-sink coordination and adequate reserve levels is critical for enhancing resilience in perennial fruit crops (Martínez-Vilalta *et al.*, 2016).

Overall, climate change highlights that sink function, transport processes, and reserve dynamics may be more vulnerable to environmental stress than photosynthetic carbon supply alone. A mechanistic understanding of source-sink interactions under multiple climate stressors is essential for developing climate-smart and resilient fruit production systems. An integrated summary of the effects of major climate stressors on source-sink dynamics, carbon allocation, and fruit crop performance is presented in Table 1.

X. ORCHARD MANAGEMENT STRATEGIES FOR OPTIMIZING CARBON ALLOCATION

Carbon allocation in fruit crops is strongly influenced by orchard management practices that affect source capacity, sink strength, phloem transport, and reserve accumulation. Sustainable productivity depends on balancing vegetative growth, reproductive demand, and carbohydrate reserves rather than maximizing carbon assimilation alone (Pawar *et al.*, 2019).

TABLE 1

EFFECTS OF CLIMATE STRESSORS ON CARBON ALLOCATION, SOURCE-SINK DYNAMICS, AND FRUIT CROP PERFORMANCE

Climate stressor	Effects on source capacity	Effects on carbon transport and partitioning	Effects on sink strength/activity	Consequences for yield and fruit quality	Representative fruit crops
Elevated CO_2	Increased photosynthesis; enhanced carbohydrate production; photosynthetic acclimation under sink limitation	Greater carbon availability; increased allocation to storage pools	Enhanced sink demand where sink capacity is sufficient	Increased yield potential but variable effects on fruit quality	Apple, grapevine, citrus
Drought	Reduced stomatal conductance and carbon assimilation	Impaired phloem loading and transport; preferential allocation to roots	Reduced cell division and expansion; reproductive abortion	Lower fruit size, yield loss, altered soluble solids	Apple, peach, mango
Heat stress	Reduced photosynthetic efficiency; accelerated leaf senescence	Increased respiratory carbon losses	Reduced pollen viability and fruit set; shortened fruit development period	Lower yield, reduced firmness, poor coloration	Apple, cherry, grapevine
Heat × drought	Severe reductions in carbon fixation and water transport	Competition among maintenance, defence, and reproductive sinks	Strong reduction in sink activity; increased fruit drop	Major yield instability and quality deterioration	Citrus, olive, almond
Elevated CO_2 × nutrient limitation	Downregulation of photosynthesis due to nutrient constraints	Reduced efficiency of carbon utilization	Restricted sink development despite carbon abundance	Limited yield gains; dilution of mineral nutrients	Apple, kiwifruit
Extreme weather events (frost, hail, flooding)	Sudden loss of photosynthetically active tissues	Disruption of source-sink connectivity	Damage to flowers, fruits, and storage organs	Immediate yield loss and long-term carry-over effects	All fruit crops

Key message: *Climate stressors affect source-sink relationships at multiple organizational levels, from carbon fixation and transport to sink utilization, ultimately determining yield stability and fruit quality.*

10.1 Canopy Management and Light Interception

Canopy architecture determines light interception, leaf area distribution, and orchard microclimate, thereby influencing photosynthetic carbon acquisition. Pruning, training systems, shoot management, and high-density planting improve canopy light distribution and optimize the leaf area-to-fruit ratio, enhancing photosynthesis while reducing unproductive vegetative growth (Lakso & Corelli Grappadelli, 1992). Improved light exposure also promotes fruit colour and sugar accumulation (Palmer *et al.*, 2013).

10.2 Crop Load Management

Crop load is a major regulator of source-sink balance. Excessive fruit numbers reduce assimilate availability, limiting fruit size, quality, and reserve replenishment (Marcelis, 1996). Fruit thinning enhances sink strength, improves return bloom, and reduces alternate bearing by preserving non-structural carbohydrate reserves (Lakso & Corelli Grappadelli, 1992; Goldschmidt, 2013). Similar benefits have been demonstrated in high-density apple orchards, where fruitlet thinning improved fruit production and quality by reducing sink competition and optimizing assimilate allocation (Mehvish Bashir *et al.*, 2023).

10.3 Irrigation and Nutrient Management

Water and nutrient availability strongly influence photosynthesis, assimilate transport, and sink activity. Regulated deficit irrigation improves water-use efficiency and fruit quality (Chaves *et al.*, 2010). Balanced nutrition supports source activity and assimilate partitioning, while foliar nutrient application enhances photosynthate distribution and delays senescence under contrasting environmental conditions (Marschner, 2012; Ghazannfar Ghani *et al.*, 2019). Excessive nitrogen, however, promotes vegetative sink demand at the expense of fruit growth. Likewise, appropriate preharvest calcium management and optimum harvest timing improve fruit quality and reduce physiological disorders, highlighting the importance of integrating nutrient management with source-sink optimization (Khan *et al.*, 2023).

10.4 Rootstock-Scion Selection and Orchard Design

Rootstocks influence carbon allocation by affecting tree vigour, hydraulic conductance, nutrient uptake, and sink demand. Size-controlling rootstocks and suitable rootstock-scion combinations improve carbon-use efficiency, fruit quality, and tolerance to environmental stresses (Tworkoski & Fazio, 2015; Warschefsky *et al.*, 2016).

10.5 Post-harvest Management and Reserve Replenishment

Post-harvest photosynthesis is essential for replenishing non-structural carbohydrate reserves required for subsequent flowering and fruiting cycles (Pawar *et al.*, 2019). Premature defoliation caused by pests, diseases, or environmental stress reduces reserve accumulation and compromises future productivity (Martínez-Vilalta *et al.*, 2016). Therefore, maintaining canopy health through appropriate post-harvest irrigation, nutrition, and pest management is critical.

An integrated framework illustrating key orchard management strategies for enhancing source capacity, optimizing sink demand, improving assimilate transport, and strengthening reserve accumulation under changing climatic conditions is presented in Figure 3.

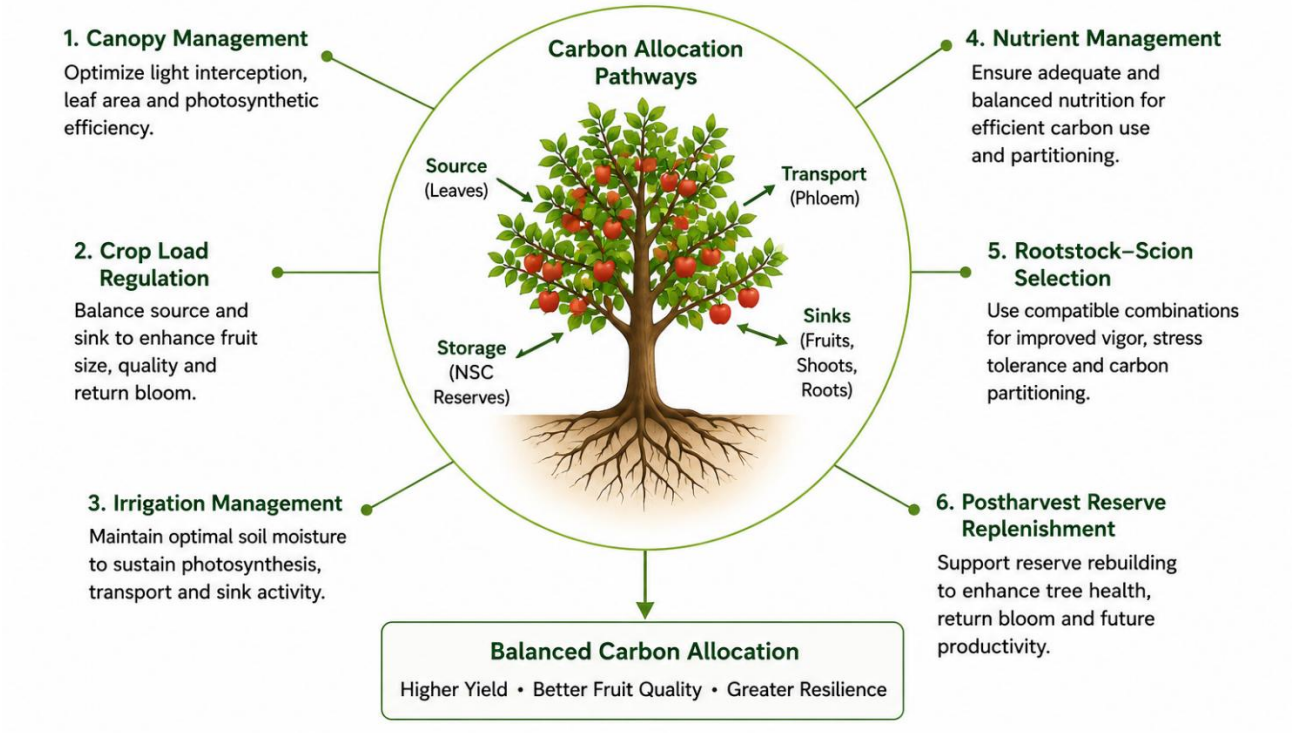

FIGURE 3: Integrated orchard management strategies for optimizing carbon allocation.

Overall, orchard practices that enhance source capacity, optimize sink demand, maintain efficient carbon transport, and preserve carbohydrate reserves provide a practical framework for improving productivity and climate resilience. Future orchard systems will increasingly rely on precision technologies and decision-support tools to dynamically manage source-sink relationships under changing environmental conditions.

XI. EMERGING TOOLS AND MODELLING APPROACHES

Advances in phenotyping, molecular biology, and computational modelling are transforming the study of carbon allocation and source-sink dynamics in fruit crops. Emerging technologies now enable the quantification, visualization, and prediction of carbon fluxes across multiple scales, supporting precision orchard management and climate resilience (Pawar *et al.*, 2019).

11.1 Isotopic Tracing and Carbon Flux Analysis

Stable isotope techniques, particularly ^{13}C-labelled CO_2, enable tracking of assimilated carbon from source leaves to fruits, roots, and storage tissues, improving understanding of carbon partitioning, reserve remobilization, and stress responses (Pallas *et al.*, 2018). Carbon isotope discrimination ($\delta^{13}C$) also provides an indicator of water-use efficiency and plant responses to drought and elevated CO_2 (Farquhar *et al.*, 1989).

11.2 High-Throughput Phenotyping and Proximal Sensing

High-throughput phenotyping using multispectral, hyperspectral, thermal, and LiDAR sensors enables non-destructive assessment of canopy architecture, photosynthetic activity, fruit load, and plant water status (Fiorani & Schurr, 2013). Integration of unmanned aerial vehicles (UAVs), proximal sensing, and machine learning supports rapid characterization of orchard variability and improves predictions of fruit yield, quality, and stress responses.

11.3 Molecular and Omics Approaches

Genomics, transcriptomics, proteomics, metabolomics, and phenomics have advanced understanding of the molecular regulation of source-sink interactions. Key targets include sucrose transporters, SWEET proteins, and sugar-signalling pathways involving trehalose-6-phosphate (T6P), sucrose non-fermenting-1-related protein kinase 1 (SnRK1), and target of rapamycin (TOR), which coordinate carbon allocation under changing environments (Chen *et al.*, 2012; Figueroa & Lunn, 2016). Genome editing technologies such as CRISPR-Cas offer opportunities to enhance source capacity, sink strength, and stress tolerance.

11.4 Functional-Structural Plant Models

Functional-structural plant models (FSPMs) integrate three-dimensional plant architecture with physiological processes to simulate carbon acquisition, transport, and allocation among competing sinks (Vos *et al.*, 2010). These models facilitate evaluation of management practices and environmental scenarios to optimize fruit growth and carbon-use efficiency (Pallas *et al.*, 2018).

11.5 Digital Agriculture and Artificial Intelligence

The integration of sensor networks, Internet of Things (IoT) technologies, cloud computing, and artificial intelligence (AI) is enabling data-driven orchard management. Machine learning algorithms increasingly combine remote sensing, omics, and environmental data to predict carbon allocation and stress responses. Digital twins—virtual representations of orchard systems updated with real-time data—offer new opportunities to optimize management under future climate scenarios.

Despite these advances, challenges remain in integrating multi-scale datasets and translating mechanistic understanding into operational decision-support tools. Future research should focus on linking molecular, physiological, and whole-orchard processes through interoperable models and standardized datasets to improve productivity, fruit quality, and resilience in climate-smart fruit production systems.

XII. RESEARCH GAPS AND FUTURE PERSPECTIVES

Despite considerable advances in understanding source-sink relationships in fruit crops, major knowledge gaps remain regarding the regulation of carbon allocation across spatial and temporal scales. Most existing frameworks are based on controlled experiments or isolated physiological processes, limiting their applicability to perennial orchard systems exposed to multiple interacting stresses (Pawar *et al.*, 2019).

12.1 From Static to Dynamic Source-Sink Frameworks

Traditional models often treat source capacity and sink strength as independent traits, whereas source-sink interactions are dynamic and feedback-regulated processes in which sink demand influences photosynthesis, assimilate transport, and reserve accumulation (Paul & Foyer, 2001). Future research should develop integrated frameworks that incorporate seasonal shifts in

sink priority, reserve remobilization, and sugar-signalling pathways, including trehalose-6-phosphate (T6P), sucrose non-fermenting-1-related protein kinase 1 (SnRK1), and target of rapamycin (TOR) (Figueroa & Lunn, 2016; Li *et al.*, 2022).

12.2 Non-Structural Carbohydrate Dynamics and Climate Stress

Although non-structural carbohydrates (NSCs) are recognized as key determinants of productivity and resilience, uncertainties remain regarding reserve thresholds, accessibility, and their role under stress conditions (Hartmann & Trumbore, 2016). Future studies should quantify organ-specific reserve pools and clarify the contributions of stored versus current assimilates to fruit development, alternate bearing, and stress recovery (Martínez-Vilalta *et al.*, 2016).

Most climate studies examine drought, heat, or elevated CO_2 individually, despite their frequent co-occurrence under field conditions (IPCC, 2023). Future research should investigate how multiple stressors affect sink activity, phloem transport, reserve dynamics, and the relative importance of carbon starvation and hydraulic failure during prolonged stress (Sevanto *et al.*, 2014).

12.3 Rootstock-Scion Interactions and Orchard Design

The influence of rootstock-scion combinations on whole-tree carbon allocation remains insufficiently understood, particularly under climate stress. Future studies should evaluate how rootstocks, orchard architecture, and management practices interact to optimize source-sink coordination and resilience (Warschefsky *et al.*, 2016).

12.4 Integrating Multi-Scale Data and Predictive Models

A major challenge is integrating molecular, physiological, and orchard-scale information into predictive frameworks (Pallas *et al.*, 2018). Combining isotopic tracing, high-throughput phenotyping, remote sensing, and omics approaches with functional-structural plant models, digital twins, and artificial intelligence-based decision-support systems could improve prediction of source-sink dynamics under diverse management and climate scenarios (Fiorani & Schurr, 2013).

12.5 Towards Climate-Smart Carbon Management

Future productivity will depend less on maximizing carbon assimilation and more on maintaining coordinated carbon flow among competing sinks across seasons (Pawar *et al.*, 2019). Research should identify traits associated with carbon-use efficiency, sink plasticity, and reserve resilience and integrate them into breeding programmes, rootstock development, and precision orchard management.

XIII. CONCLUSIONS

Carbon allocation in fruit crops is a dynamic, integrated process that underpins productivity, fruit quality, and long-term orchard performance. Yield depends not only on photosynthetic carbon supply but also on the coordinated regulation of source capacity, sink strength, phloem transport, and non-structural carbohydrate (NSC) reserves across developmental stages. Evidence indicates that sink activity actively regulates carbon assimilation through metabolic and signalling feedback, while competition among fruits, vegetative organs, and storage tissues, together with reserve accumulation and remobilization, links current carbon allocation with future productivity. Consequently, maintaining functional sink activity and adequate carbohydrate reserves is fundamental for sustaining yield stability and reducing alternate bearing.

Climate change is expected to intensify disruptions in source-sink coordination through drought, heat stress, elevated CO_2, nutrient limitations, and extreme weather events, with sink processes and phloem transport often more vulnerable than photosynthesis. Emerging approaches, including isotopic tracing, high-throughput phenotyping, omics technologies, remote sensing, and functional-structural modelling, provide unprecedented opportunities to quantify and predict carbon dynamics in perennial fruit crops. Their integration with precision orchard management, optimized rootstock-scion combinations, and climate-smart practices will facilitate resilient production systems.

For researchers, priority areas include developing dynamic source-sink models that incorporate seasonal shifts and stress responses, quantifying organ-specific reserve thresholds, and understanding the molecular basis of sink plasticity. **For breeders**, traits associated with carbon-use efficiency, sink strength, and reserve resilience should be integrated into breeding programmes. **For orchard managers and advisors**, practical strategies include optimizing crop load through thinning, managing canopy architecture for improved light interception, implementing deficit irrigation strategies, maintaining post-harvest canopy health for reserve replenishment, and adopting precision technologies for monitoring carbon status. **For policymakers**, supporting research on climate-resilient rootstocks and varieties, promoting adoption of climate-smart

management practices, and investing in extension services that translate source-sink science into actionable recommendations are essential priorities.

Ultimately, future gains in fruit productivity and quality will depend not on maximizing carbon assimilation alone, but on optimizing whole-plant carbon economy through integrated, predictive, and multi-scale management of source-sink interactions, reserve dynamics, and environmental responses.

DATA AVAILABILITY STATEMENT

No new data were generated or analysed in support of this review. Data sharing is not applicable to this article.

CONFLICTS OF INTEREST

The authors declare that there are no conflicts of interest regarding the publication of this review article.

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