

# The roles of non-structural carbohydrates in fruiting: a review focusing on mango (*Mangifera indica*)

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## ABSTRACT

Reproductive development of fruiting trees, including mango (*Mangifera indica* L.), is limited by non-structural carbohydrates. Competition for sugars increases with cropping, and consequently, vegetative growth and replenishment of starch reserves may reduce with high yields, resulting in interannual production variability. While the effect of crop load on photosynthesis and the distribution of starch within the mango tree has been studied, the contribution of starch and sugars to different phases of reproductive development requires attention. This review focuses on mango and examines the roles of non-structural carbohydrates in fruiting trees to clarify the repercussions of crop load on reproductive development. Starch buffers the plant's carbon availability to regulate supply with demand, while sugars provide a direct resource for carbon translocation. Sugar signalling and interactions with phytohormones play a crucial role in flowering, fruit set, growth, ripening and retention, as well as regulating starch, sugar and secondary metabolites in fruit. The balance between the leaf and fruit biomass affects the availability and contributions of starch and sugars to fruiting. Crop load impacts photosynthesis and interactions between sources and sinks. As a result, the onset and rate of reproductive processes are affected, with repercussions for fruit size, composition, and the inter-annual bearing pattern.

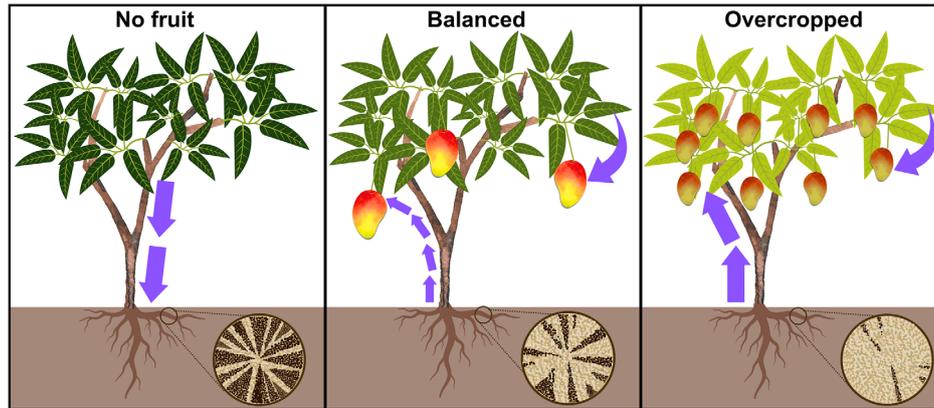
**Keywords:** carbohydrate metabolism, carbon allocation, crop physiology, flowering, fruit development, hormonal regulation, starch, sugar sensing, yield.

## Introduction

Plants use atmospheric carbon for biosynthesis of structural carbohydrates (SC) and non-structural carbohydrates (NSC). SC, such as cellulose and hemicellulose, are used for constructing and strengthening plant tissues, including stems and cells (Hartmann and Trumbore 2016). Shorter-chain NSC (i.e. starch and sugars) contribute to carbon translocation, energy production, metabolic processes, osmotic regulation and control of vegetative and reproductive development (Loescher *et al.* 1990; Smeekens *et al.* 2010; Dominguez and Niittylä 2022). Temporal variability in NSC concentrations is well-studied in deciduous trees and vines grown in temperate climates, notably fruit and nut crops (Boldingh *et al.* 2000; Holzapfel *et al.* 2010; Rossouw *et al.* 2017b; Mesa *et al.* 2019; Breen *et al.* 2020; Tixier *et al.* 2020). To a lesser extent, NSC dynamics have been explored for evergreen fruit trees in tropical or sub-tropical environments (Davie and Stassen 1997b; Olesen *et al.* 2008; Singh *et al.* 2017).

In mango (*Mangifera indica* L.), our understanding of NSC utilisation is incomplete. However, variability in starch across organs at key phenological stages has been described (Davie and Stassen 1997a; Stassen and Janse van Vuuren 1997; Davie *et al.* 1999; Normand *et al.* 2009), as has the abundance of major sugars (Normand *et al.* 2006; Prasad *et al.* 2014). Understanding NSC in mango trees is important for enhancing fruit productivity.

Starch, the bulk of NSC, is stored as reserves to be degraded and mobilised to increase the pool of usable sugars (Fig. 1). Leaf storage of starch is typically transient whereas storage in perennial woody structures such as roots and branches are more long term (Normand *et al.* 2009). Starch regulates carbon utilisation indirectly whereas sugars influence organ growth directly (Stitt and Zeeman 2012). Research in mango has focused on starch, partly due to



**Fig. 1.** Conceptual distribution of photosynthates and remobilisation of root starch reserves during fruit development. The bottom right wagon wheels show root transverse sections with dark brown starch deposits in xylem parenchyma cells. Left: in the absence of fruit, sugars are translocated from leaves to roots, forming elevated root starch reserves. Centre: with a balanced canopy, leaves provide sugars for fruit growth, and root starch reserves support peak sink demands. Optimal allocation of resources ensures both fruit development and leaf function. Leaf chlorophyll content remains stable as fruits mature. Right: overcropped trees rely more on root starch for fruit growth, depleting reserves. Increased competition for resources may lead to smaller fruit and reduced leaf chlorophyll, resulting in pale green leaves.

the relative ease of quantification (Smith and Zeeman 2006). Methods quantifying individual sugars are usually more sophisticated (Ma *et al.* 2014; Georgelis *et al.* 2018).

Sugar concentrations are typically less than starch (Smith and Stitt 2007; Smeekens *et al.* 2010). Sugars supply structural units for organic compounds, including proteins and amino acids, and secondary metabolites such as colour and flavour compounds (Priestly 1962). Sucrose, glucose and fructose concentrations differ between cultivars, tissues and developmental stages (Li *et al.* 2020). Sucrose, as the predominant transported carbon form from sources to sinks, is integral for resource allocation (Chauhan and Pandey 1984). Sucrose is the principal sugar found in mango fruit, whilst fructose, followed by glucose, are usually the most abundant reducing sugars (Medlicott and Thompson 1985; Malundo *et al.* 2001).

Source–sink organ relations dictate sugar flow. In mango, fruit is the predominant sink, importing sugars irrespective of the number of supporting leaves (Chacko *et al.* 1982). Source organs, like photosynthesising leaves or storage tissues, should be considered in conjunction with fruit biomass when assessing carbohydrate source and sink organ relations (Roper and Loescher 1987; Kliwer and Dokoozlian 2005; Wünsche and Ferguson 2010). Crop load, the number and size of the fruit produced per tree or branch unit (Wünsche and Ferguson 2010), influence NSC use by sinks. Excessive yield depletes NSC reserves beyond the tree's recharge capacity, diminishing reproductive development the following season (Capelli *et al.* 2016) (Fig. 1). An excessive crop load delays fruit maturation, and lead to smaller and inferior quality fruit (Simmons *et al.* 1998). Low yield promotes NSC

allocation towards reserve storage and may stimulate vegetative growth (Erf and Proctor 1987; Blanco *et al.* 1995; Berman and DeJong 2003).

Starch concentrations in mango roots, wood, bark, shoots and leaves tend to decrease in winter, during flowering, fruit set and the spring vegetative flush (Stassen and Janse van Vuuren 1997; Davie *et al.* 1999). Root and wood starch negatively correlates with fruit growth (Davie and Stassen 1997a), with greater crop loads reducing starch reserves as fruit draws carbohydrates from alternative sinks (Davie and Stassen 1997b) (Fig. 1).

This review examines NSC dynamics in fruit trees, emphasising the roles of NSC in fruit development and productivity. It explores NSC types and their roles in reproductive development, the importance of leaf photosynthesis for fruiting including crop load effects, and NSC allocation between sources and sinks. Proposing future research areas, this review uses mango as a case study, incorporating resources from fundamental plant studies and other fruiting species for comprehensiveness.

### Types of NSC and their roles in fruiting

NSC exist in plants in two primary forms: (1) starch; and (2) sugars (Table 1). Starch molecules are not osmotically active, meaning they cannot be translocated and are used for carbon storage (Lalonde *et al.* 1999). Starch is converted to sugars to allow mass flow along the sieve tubes of the phloem. At the sink, sugars and water are unloaded into expanding or storage cells where they are metabolised for growth, storage, or as signals for biochemical processes. Partitioning of carbon

**Table 1.** Key characteristics of non-structural carbohydrates (NSC) in fruit trees.

	<b>Starch</b>	<b>Sucrose</b>	<b>Hexoses (glucose and fructose)</b>	<b>Low abundance sugars and polyols</b>
Phloem mobility	Immobile <sup>A,B</sup>	Mobile (primary transport sugar) <sup>A,B</sup>	Mobile <sup>A,B</sup>	Mobile <sup>A,B</sup>
Structural classification	Polysaccharide, composed of glucose monomers <sup>B,C</sup>	Disaccharide, composed of a glucose and fructose monomer <sup>B,C</sup>	Monosaccharides <sup>B,C</sup>	Monosaccharides (e.g. galactose), disaccharides (e.g. trehalose), oligosaccharides (e.g. raffinose), polyols (e.g. myo-inositol), phosphorylated intermediates (e.g. trehalose-6-phosphate) <sup>B,C</sup>
Leaf origin and utilisation	Synthesised and stored at day, degraded and exported at night <sup>B,D</sup>	End-product of photosynthesis or synthesised from starch <sup>B,D</sup> . Metabolised, converted to starch or exported <sup>B,D</sup>	End-products of photosynthesis or synthesised from starch <sup>B</sup> . Metabolised or exported <sup>B</sup>	Products of photosynthesis (e.g. maltose) or synthesised (e.g. myo-inositol) <sup>D,E,F,G</sup> . Metabolised or exported <sup>E,F</sup>
Fruit origin and utilisation	Synthesised during fruit growth, degraded during late maturation and ripening <sup>H,I</sup>	Imported or synthesised from starch <sup>B,J,K</sup>	Imported or synthesised during ripening <sup>B,K</sup>	Imported or synthesised and metabolised <sup>B,L,M</sup>
Root and wood origin and utilisation	Synthesised when leaf assimilate supply outweighs sink demand, remobilised when carbon demand outweighs leaf supply <sup>N,O,P</sup>	Imported or synthesised from starch and metabolised <sup>B,O,P,Q</sup>	Imported or synthesised from starch and metabolised <sup>B,O,Q,R</sup>	Imported or synthesised and metabolised <sup>M,O,Q</sup>
Key roles in reproductive development	Degradation and remobilisation regulate carbon availability for floral induction, flowering, fruit set, retention and growth. <sup>S,T,U</sup>	Carbon transport to buds, flowers and fruit for growth, energy generation and signalling <sup>B,S,T</sup>	Supply to buds, flowers and fruit, used for growth, energy generation and signalling <sup>B,E,S,T</sup>	Provides signalling to regulate reproductive processes including flowering, fruit growth and ripening <sup>E,F,G,T</sup>
Other roles	Reserve storage and remobilisation for respiration and vegetative growth <sup>V,W</sup>	Long distance carbon transport. <sup>A,B</sup> Signalling for gene expression, cellular growth, vegetative developmental processes, carbon metabolism and abiotic stress responses. <sup>E,X,Y,Z</sup> Cellular osmotic regulation. <sup>A,G</sup>	Resources for cellular respiration. <sup>B,C</sup> Utilised for synthesis of structural carbohydrates and carbon translocation. <sup>B,X,Y</sup> Facilitate cellular and osmotic regulation. <sup>B,Y</sup>	Carbon translocation, cellular osmotic protection and regulation, stabilisation of enzymes and cell membranes. <sup>E,X,Y</sup> Signalling for gene expression, abiotic stress mitigation, carbon metabolism and vegetative development. <sup>E,X,Y</sup>

<sup>A</sup>Dominguez and Niittylä (2022).<sup>B</sup>Taiz *et al.* (2015).<sup>C</sup>Bowsher *et al.* (2008).<sup>D</sup>Zeeman *et al.* (2007).<sup>E</sup>Eveland and Jackson (2012).<sup>F</sup>Valluru and Van den Ende (2011).<sup>G</sup>Smeekens *et al.* (2010).<sup>H</sup>Davie *et al.* (1999).<sup>I</sup>Stassen and Janse van Vuuren (1997).<sup>J</sup>Chauhan and Pandey (1984).<sup>K</sup>Léchaudel and Joas (2006).<sup>L</sup>Li *et al.* (2020).<sup>M</sup>Noiraud *et al.* (2001).<sup>N</sup>Davie and Stassen (1997b).<sup>O</sup>Loescher *et al.* (1990).<sup>P</sup>Rossouw *et al.* (2017b).<sup>Q</sup>Rossouw *et al.* (2017a).<sup>R</sup>Normand *et al.* (2006).<sup>S</sup>Capelli *et al.* (2021).<sup>T</sup>Durán-Soria *et al.* (2020).<sup>U</sup>Lloyd and Kossmann (2019).<sup>V</sup>MacNeill *et al.* (2017).<sup>W</sup>Stitt and Zeeman (2012).<sup>X</sup>Cierieszko (2018).<sup>Y</sup>Gibson (2005).<sup>Z</sup>Sami *et al.* (2016).

between starch and sugars is regulated by carbon supply and demand signalling (Smith and Stitt 2007; Eveland and Jackson 2012; Stitt and Zeeman 2012).

## Starch

Starch is a storage polyglucan that accumulates as granules of amylose or amylopectin in the plastids of cells. Starch acts as a resource for reserve mobilisation to sinks when demand is greater than production (Davie *et al.* 1999; Normand *et al.* 2009). In mango, starch is mainly found in xylem parenchyma of roots, the trunk, branches and shoots, and accounts for more than 80% of the NSC (Davie *et al.* 1999; Normand *et al.* 2006; Normand *et al.* 2009).

Starch synthesis and degradation regulate distribution of NSC between sources and sinks. Synthesis is conserved amongst plant species suggesting a common evolutionary origin. For an overview of the biochemical process of starch formation in plant cells, see the review by Pfister and Zeeman (2016). In contrast, the degradation of starch varies across species and between organs (Smith *et al.* 2005). In leaves, the primary NSC source, starch synthesis and degradation are regulated by enzymes, diurnally by circadian fluctuations (Kötting *et al.* 2010). Starch in the leaf accumulates in the chloroplasts during the day and is converted to sucrose at night to allow continued export to sinks, and to provide carbon skeletons and energy within the leaf cells (Smith *et al.* 2005; Stitt and Zeeman 2012). In perennial storage organs, such as roots and wood, starch synthesis and degradation are dependent on developmental processes and source-sink relations (Kötting *et al.* 2010; MacNeill *et al.* 2017; Rossouw *et al.* 2017a) (Fig. 1). In leaves and the perennial structures, starch is catalysed by amylases and debranching enzymes (Smith *et al.* 2005; Stitt and Zeeman 2012).

## Soluble sugars

Sugars are involved in carbon translocation and act as structural components, cell nutrients and as signals for growth and development (Eveland and Jackson 2012). In mango and most other higher plants, sucrose is the main long-distance transport sugar. In developing fruit, sucrose is degraded to the hexoses, glucose and fructose, or their derivatives (Ruan 2012; Durán-Soria *et al.* 2020; Li *et al.* 2020). Numerous minor sugars, and polyols (sugar alcohols), including raffinose, trehalose, *myo*-inositol, mannitol, xylose and maltose also contribute to developmental or other physiological processes such as abiotic stress mitigation in plants (Pandey 1974; Iturriaga *et al.* 2009; Valluru and Van den Ende 2011).

The availability of sugars controls growth, both as immediate substrates for metabolism and as signalling molecules (Smeekens *et al.* 2010). Sugar signals allow plants to modulate site-specific and whole-plant growth, thereby coordinating development (Smeekens *et al.* 2010; Eveland and Jackson 2012). Sucrose signalling occurs directly through binding to sugar sensors or indirectly as hexose signals, a product of

sucrose cleavage (Rolland *et al.* 2006; Eveland and Jackson 2012). Hexoses exhibit a greater signalling potential for promoting organ growth and cell proliferation, whereas sucrose signalling is associated with cell differentiation and maturation (Eveland and Jackson 2012). Minor sugars and polyols, notably *myo*-inositol, trehalose and raffinose also play roles in sugar signalling (Iturriaga *et al.* 2009; Valluru and Van den Ende 2011).

As a resource for energy and carbon, sugars are essential for all developmental processes in plants (Rolland *et al.* 2006; Eveland and Jackson 2012; Sami *et al.* 2016; Ciereszko 2018; Aluko *et al.* 2021). As such, vegetative growth, flowering, fruit set, fruit growth and retention, and plant adaptation to challenging environmental conditions, are dependent on the plant's sugar status. Sugar accumulation contributes to the maintenance of cell turgor potential, generating a gradient for water uptake into the cells and cell expansion (Boyer 1988; Rhodes and Samaras 1994).

In vegetative tissues, sugars trigger the proliferation of vegetative organs and produce larger and thicker leaves (Gibson 2005). Additionally, sugars are involved in leaf senescence, (Rolland *et al.* 2006; Kim 2019). The initiation of leaf senescence is marked by appropriate sugar signals, followed by tightly regulated temporal changes in sugars to supply carbon-mediated energy needed for the senescence processes (Kim 2019). Leaf senescence compensates for energy starvation, the breakdown of organelles such as chloroplast, and loss of photosynthetic activity. As primary cellular energy metabolites, sugar signalling and metabolism govern the induction and progression of leaf senescence.

The availability of NSC regulates canopy development and the balance between leaf and fruit biomass. Leaf-to-fruit ratio, in turn, determines mango fruit growth, regulating NSC concentrations in the tree, completing the feedback loop (Lechaudel *et al.* 2002; Léchaudel and Joas 2007).

As osmotically active solutes, sugars including sucrose, glucose and fructose, play important roles during abiotic stress conditions including drought, salinity and cold stress (Sami *et al.* 2016). During stress, these sugars stimulate the osmotic movement of water into cells, raising osmotic pressure. Certain sugars are also osmo-protective, including the raffinose family of oligosaccharides, mainly raffinose, stachyose and verbascose, which accumulates in leaves when plants are exposed to abiotic stresses (Sami *et al.* 2016). They stabilise proteins and interact with cell membranes to prevent denaturation of proteins under drought and other environmental constraints (Rontein *et al.* 2002). Fructans are indirectly involved in the osmotic adjustment of plant cells, while trehalose functions as an osmolyte (Sami *et al.* 2016). Both these sugar types also stabilise membranes, and their accumulation consequently provides osmo-protection for cells.

## Sucrose

Sucrose metabolism in fruit and other sinks is self-regulating via starch biosynthesis and sucrose degradation

metabolic pathways (Ruan *et al.* 2012; Durán-Soria *et al.* 2020). High sucrose concentrations in phloem, resulting from decreased sink demand or an oversupply from the leaves, reduce subsequent sugar loading to the phloem, and NSC accumulate in the surrounding leaf mesophyll cells (Chiou and Bush 1998). Carbohydrate accumulation in the mesophyll, in turn, downregulates photosynthesis. Strong sinks drain sucrose from the phloem creating osmotic pull through phloem loading and decrease sucrose in mesophyll cells to stimulate photosynthesis.

### Hexoses

Sucrose cleavage is crucial to allocate carbon between sources and sinks, as well as in the initiation of hexose-based sugar signals (Koch 2004). The glucose and fructose signals modulate the expression of various genes, including those involved in the biosynthesis and perception of hormones such as abscisic acid (ABA). Invertases, enzymes responsible for sucrose cleavage, trigger the initiation and expansion of sinks by modifying the nature of sugar signals from sucrose to hexoses (Sturm and Tang 1999; Koch 2004). During the expansion of organs, changes in the hexose-to-sucrose ratio impact the transition of sinks to storage and maturation. Accordingly, the hexose-to-sucrose ratio regulates the growth and ripening of fruit (Lee *et al.* 2021).

### Trehalose-6-phosphate (T6P)

T6P is a minor sugar that acts as a potent signal in plants, playing a key role in regulating sucrose levels (Figuroa and Lunn 2016; Durán-Soria *et al.* 2020; Fichtner and Lunn 2021). T6P regulates the production of sucrose in source organs against sink demand. Additionally, T6P regulates sucrose utilisation in sink organs for growth or storage. In *Arabidopsis thaliana* L., there is a reduction in T6P concentration when carbon starvation occurs, signalling low sucrose availability (Lunn *et al.* 2014). In contrast, increased T6P concentration in leaves inhibits the remobilisation of transitional starch to sucrose (Fichtner and Lunn 2021). Yadav *et al.* (2014)

indicated that T6P has a dual function as a signal and negative feedback regulator of sucrose. In addition, T6P metabolism in guard cells influences stomatal conductance, meaning T6P may affect photosynthesis (Figuroa and Lunn 2016).

T6P may regulate development by signalling the plant's capacity to supply sucrose for upcoming development (Fichtner and Lunn 2021). In reproductive development, there is a connection between T6P and the timing of flowering (Figuroa and Lunn 2016). In the buds of mandarin (*Citrus reticulata* L.), trehalose metabolism associated genes were upregulated in years when cropping was limited by flowering (Shalom *et al.* 2012). In some species such as cucumber (*Cucumis sativus* L.), pre-existing fruit inhibit the growth of subsequent fruit (Smith and Samach 2013; Zhang *et al.* 2015). High concentrations of T6P in the first fruit increase sink strength to the detriment of the others.

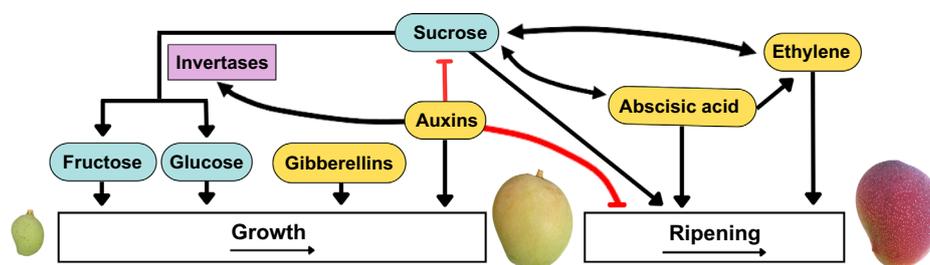
### Phytohormone-sugar crosstalk

Phytohormones control growth and development in plants (Weyers and Paterson 2001). Sugars interact with phytohormones to form a network for regulating development, including fruiting (León and Sheen 2003; Durán-Soria *et al.* 2020) (Fig. 2). Interactions between sugars and phytohormones ensure that hormone-driven processes are compatible with plant carbon status (Ljung *et al.* 2015). Responses that promote growth can be depressed under limited availability of NSC.

### ABA and ethylene

Phytohormones, such as ABA and ethylene, have crucial roles in fruit growth, ripening and senescence (Lin *et al.* 2009; Gupta *et al.* 2022). During ripening in climacteric and non-climacteric fruit, ABA regulates ethylene biosynthesis and signalling (Gupta *et al.* 2022).

Sugar signalling is a key regulator of ripening in climacteric and non-climacteric fruit (Cherian *et al.* 2014). In strawberry (*Fragaria × ananassa* L.), sucrose stimulates ABA production and facilitates ripening (Jia *et al.* 2013; Luo *et al.* 2020). In



**Fig. 2.** Interaction between sugar and phytohormones during fruit growth. Gibberellins and auxins promote fruit growth through cell division and expansion. Auxins inhibit sucrose accumulation and stimulate the degradation of sucrose to fructose and glucose via invertase, enhancing growth. Auxins also delay ripening. Sucrose promotes ripening and stimulates abscisic acid (ABA) and ethylene biosynthesis, while ABA and ethylene enhance sucrose accumulation. ABA also regulates ethylene biosynthesis. Adapted from Durán-Soria *et al.* (2020).

apple (*Malus domestica* L.), ABA signals sugar transport and starch degradation to promote sugar accumulation in fruit (Ma *et al.* 2017). The interaction between ABA and sugar signalling for mango ripening has received little attention. However, ABA–sugar crosstalk possibly affects flower induction (Upreti *et al.* 2013).

In mango and other climacteric fruit, ethylene is the dominant regulator of ripening (Tharanathan *et al.* 2006; Chen *et al.* 2018). Ethylene promotes sucrose accumulation in fruit, and exogenous ethylene advances sugar accumulation (Chidley *et al.* 2017). Similarly, exogenous sucrose stimulates ethylene biosynthesis (Durán-Soria *et al.* 2020). Finally, exogenous ABA accelerates ripening and ethylene biosynthesis (Zaharah *et al.* 2013). ABA, ethylene and sugar all interact to affect ripening in mango (Wu *et al.* 2022).

### Gibberellins, auxins and other phytohormones

During early fruit development, gibberellins and auxins promote cell division and expansion, determining fruit size (Devoghalaere *et al.* 2012; El-Sharkawy *et al.* 2017; He and Yamamuro 2022). Other hormones, such as cytokinins, brassinosteroids, jasmonic acids and strigolactones are also involved (Kumar *et al.* 2014). Cytokinins regulate fruit growth by promoting cell division, while brassinosteroids and jasmonic acids affect ripening.

Decreases in the concentration of gibberellins are important for NSC accumulation in mango buds and for flowering (Das *et al.* 2019). The growth regulator paclobutrazol, a gibberellin inhibitor, is applied to broad-acre and tree crops, including mango, to reduce vegetative growth and to induce flowering. Paclobutrazol inhibits gibberellin synthesis by blocking the oxidation of *ent*-kaurene (Sponsel 1995), prompting an increase in sucrose concentrations in mango shoots (Rahim *et al.* 2011). By inhibiting vegetative growth, paclobutrazol increases the concentrations of stored NSC in trees, favouring fruit development (Yeshitela *et al.* 2004; Menzel and Le Lagadec 2017).

Auxins and jasmonic acids are two additional phytohormones that interact with sugars to influence reproductive development in fruiting crops, as discussed by Durán-Soria *et al.* (2020). Auxins stimulate invertase activity, which catalyses the hydrolysis of sucrose into glucose and fructose (Morris and Arthur 1984). However, specific roles of auxins and jasmonic acids in reproductive development remain largely unknown. Their involvement in NSC metabolism may be more indirect, possibly mediated through interactions with ABA and/or ethylene.

### Pigments

Anthocyanins and carotenoids contribute to the colour of fruit (Ranganath *et al.* 2018). Anthocyanins are flavonoids, and accumulate in mango peel, providing a red colour, while carotenoids are responsible for yellow or orange colours and accumulate in the peel and flesh (Ni *et al.* 2022). The

shikimate pathway, the foundation for flavonoid biosynthesis, consumes 20–50% of the carbon fixed by plants, making it a substantial carbon sink (Tohge *et al.* 2013). Crosstalk between sugars and phytohormones modulates anthocyanin biosynthesis in the presence of light (Das *et al.* 2012).

In *Arabidopsis*, exogenous sucrose upregulates genes in the phenylpropanoid pathway inducing anthocyanin synthesis (Das *et al.* 2012; Durán-Soria *et al.* 2020). In kiwifruit (*Actinidia deliciosa* L.), Nardozza *et al.* (2020) showed that carbon starvation following girdling, reduced the concentration of sucrose and T6P, and caused a transcriptionally induced cessation of anthocyanin synthesis in fruit. It was suggested that T6P availability may affect anthocyanin biosynthesis. Lueangprasert *et al.* (2010) found that applying fructose to mango peel stimulated anthocyanin, especially on the sun exposed sections of the fruit.

Carotenoids are involved in the absorption of energy for photosynthesis and the protection of chlorophyll from excessive light (Armstrong and Hearst 1996). In mango peel, carotenoid accumulation occurs when chloroplasts develop into chromoplasts (Medlicott *et al.* 1986; Cheung *et al.* 1993). Carotenoid and sugar accumulation in fruit is concomitant (Li and Yuan 2013). In mandarin, exogenous sucrose to peels accelerates the breakdown of chloroplasts to chromoplasts (Iglesias *et al.* 2001). Sucrose regulates carotenoid metabolism through the regulation of carotenoid biosynthesis genes (Sadali *et al.* 2019). For example, starch conversion into sugars during tomato (*Solanum lycopersicum* L.) fruit ripening is correlated with carotenoid accumulation (Li and Yuan 2013). Sucrose depletion in tomato influences expression of *PSY1*, a gene involved in carotenoid accretion, thereby delaying carotenoid accumulation (Télef *et al.* 2006). Sugar starvation, for example, as induced by defoliation inhibits the accumulation of carotenoid in the fruit (Li and Yuan 2013).

### Leaves: the main source

Fully expanded mature leaves are the primary source of NSC in trees. For NSC to be used for growth, they must be generated in the leaves and transported to a sink (Kozłowski 1992; Blanke 2009). Photosynthesis and sugar export are upregulated under low sugar levels, under strong fruiting or vegetative growth (Rolland *et al.* 2006).

### Carbon assimilation

#### Photosynthesis

Synthesis of NSC in plants starts with photosynthesis. Light is converted to chemical energy in the form of adenosine triphosphate (ATP) and nicotinamide adenine dinucleotide phosphate (NADPH) by chlorophyll (Avenson *et al.* 2005). The chemical energy is used to convert CO<sub>2</sub> and water into sugars. Mango peel contains chlorophyll, particularly early in development. However, the rate of photosynthesis is low

compared with that occurring in the leaves (Chauhan and Pandey 1984). The carbon that is fixed during photosynthesis can be metabolised to provide energy and carbon skeletons for respiration and growth or is stored as reserves.

The greater the rate of photosynthesis, the more sucrose is exported and is available for sinks (Ho 1976; Lanoue *et al.* 2018). Starch is produced when sucrose formation exceeds the capacity for export or the demand for NSC from sinks (Zeeman *et al.* 2007; Weise *et al.* 2011). Starch can be degraded and converted back to sucrose when the demand for sugar outweighs supply, for example, during the night (Zeeman *et al.* 2007).

The rate of photosynthesis is affected by phenology and the temperature, humidity and light (Pessaraki 1996; Kaiser *et al.* 2015). Net photosynthesis ( $A_{\text{net}}$ ) in  $C_3$  species such as mango is a balance between the  $\text{CO}_2$  fixation and respiration (Tcherkez and Limami 2019). Stomatal conductance ( $g_s$ ) controls  $A_{\text{net}}$  in mango with a high  $g_s$  corresponding with high  $A_{\text{net}}$  (Urban *et al.* 2002, 2006; Lu *et al.* 2012).

Photosynthetic capacity ( $A_{\text{max}}$ ) refers to the maximum rate at which a leaf can fix carbon (Smith *et al.* 2019). The leaf nitrogen concentration, although not strictly determining  $A_{\text{net}}$ , may be rate limiting and regulates  $A_{\text{max}}$  of mango (Urban *et al.* 2003).  $A_{\text{max}}$  is related to leaf nitrogen because the proteins of the Calvin cycle and thylakoids represent the majority of leaf nitrogen (Evans 1989). Leaf nitrogen concentration per unit area exhibits a positive non-linear relationship with  $A_{\text{max}}$  regarding maximum carboxylation rate ( $V_{\text{cmax}}$ ), electron transport capacity ( $J_{\text{max}}$ ), rate of phosphate release in triose phosphate utilisation (TPU), and dark respiration (Urban *et al.* 2003).

The regulation of photosynthesis is linked to leaf NSC concentration and composition (Goldschmidt and Huber 1992; Paul and Pellny 2003; Lloyd and Zakhleniuk 2004). Accumulation of end-products such as starch, sucrose, and hexose sugars introduces negative feedback, downregulating  $A_{\text{max}}$  and disrupting gene expression (Goldschmidt and Huber 1992). Inorganic phosphate (Pi) further complicates this regulation, with the rate of end-product synthesis determining the recycling of Pi back into the photosynthetic reaction, potentially leading to feedback inhibition (Paul and Pellny 2003). Pi recycling is closely intertwined with leaf carbon metabolism. Although the hexose-to-sucrose ratio may influence photosynthesis, the specific relationships with expression of photosynthetic genes remain elusive (Lloyd and Zakhleniuk 2004). The ambiguity extends to the relative impact of hexose or sucrose accumulation on photosynthetic inhibition (Lobo *et al.* 2015).

### Respiration

Respiration occurs where sugars are converted to energy for cell division, expansion, senescence, translocation and the storage of metabolites (Jackson 2003). For mango and other  $C_3$  plants, 30–60% of photosynthates are consumed by respiration (Kozłowski 1992; Fischer *et al.* 2013;

Amthor *et al.* 2019). Respiration can be divided by function as tissue maintenance or growth (Fischer *et al.* 2013), or by light dependence as photorespiration or dark respiration. Maintenance respiration occurs in all tissues and affects the dynamics of NSC in fruiting crops. Maintenance respiration is a priority over growth when photosynthates are limited (Génard *et al.* 2008).

The effect of fruit on dark respiration in leaves is inconclusive. Wünsche and Ferguson (2010) found that fruiting increases dark respiration in apple, whereas Watson *et al.* (1978) found the opposite. In grapevine (*Vitis vinifera* L.), respiration in fine roots was higher in plants without fruit likely because root activity was downregulated under higher crop load (Morinaga *et al.* 2003).

Prior to harvest, respiration in mango fruit increases along with an increase in soluble solids (Léchaudel and Joas 2006). There is a negative relationship between respiration and postharvest shelf life (Ravindra and Goswami 2008).

### Leaf source activity

Although leaves are the primary source for NSC, the contribution of individual mango leaves vary (Chacko *et al.* 1982). Young expanding leaves are net sinks compared with older leaves which are sources (Zude and Luedders 1997; Fischer *et al.* 2013). Photosynthesis eventually starts to decline in old senescent leaves (Karim *et al.* 1999).

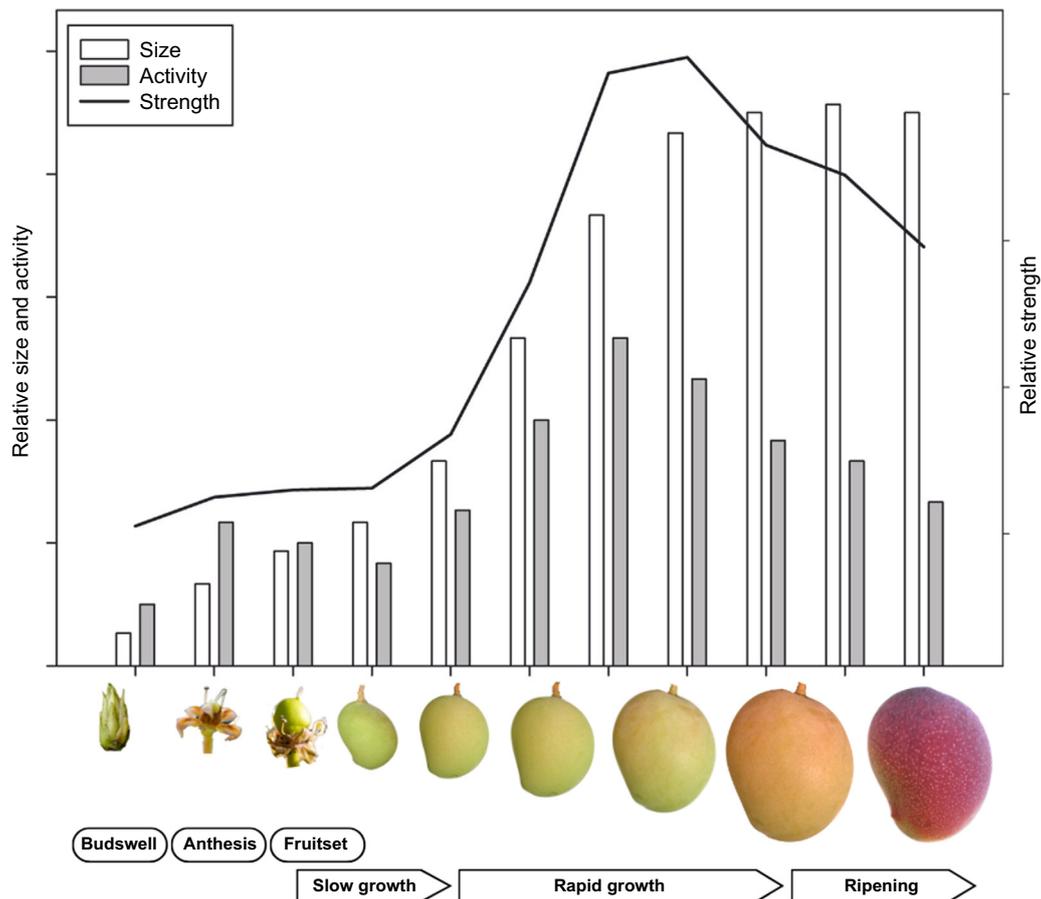
In mango, the leaves export sucrose in both acropetal and basipetal directions, with acropetal transport dominant during flowering and fruit development, and basipetal transport dominant during flower bud differentiation (Chauhan and Pandey 1984). The translocation of sugars to fruit peaks when fruit are half-grown to fully-grown.

### Fruit: the predominant sink

Sink strength indicates the ability to import sugars compared with other sinks and is the product of sink size and activity (Marcelis 1996; Bihmidine *et al.* 2013). Sink strength represents the maximum rate a tissue can accumulate dry matter (Génard *et al.* 2008). Sink activity is governed by phloem unloading and transport and absorption of sugars into sink cells (Génard *et al.* 2008). Ultimately, sinks utilise NSC for respiration, growth and storage (Pawar and Rana 2019).

Mango fruit have different sink strength during development (Fig. 3). The fruit exhibits a sigmoid pattern of growth, with slower initial growth followed by several months of rapid growth before the fruit stabilise (Simmons *et al.* 1998). Carbon isotope tracing showed that the sink strength peaks when fruit are half-grown to fully-grown (Chauhan and Pandey 1984). Flower buds and marble sized fruit are weak sinks, whereas flowers and pea-sized fruit are intermediate.

In mature mangoes, NSC represent 90–94% of the dry mass, with the rest being organic acids, lipids and proteins



**Fig. 3.** A model depicting the evolution of reproductive sink size, activity, and strength from budswell to fruit ripening in mango. Based on insights from Chauhan and Pandey (1984) and Simmons *et al.* (1998).

(Bello-Pérez *et al.* 2007). NSC levels are stable in the initial fruit growth, however, accumulation of NSC primarily occurs as starch during rapid growth (Tandon and Kalra 1983). The rate of starch accumulation and amylase activity matches the growth rate, slow initially, rapid intermediately and plateauing before maturity. As the fruit ripen, sugars, primarily sucrose, accumulate as a result of the hydrolysis of starch (Malundo *et al.* 2001). Fruit should be harvested at the right stage when starch is converting to sugar to maintain quality and shelf life (Simão *et al.* 2008; Yu *et al.* 2022). Fruit starch maintain shelf life by providing carbon for respiration. Starch also contributes to fruit firmness, with the fruit softening when the starch is converted to sugars, improving sweetness and flavour.

Individual fruit compete for NSC, along with growing shoots, roots and leaves (Pawar and Rana 2019). The proximity of the sink to the source is important in determining a sink's competitive ability (Patrick 1988). Active sinks on a branch are fed by the nearest sources provided sources are sufficient to meet sink activity (Sprugel *et al.* 1991). Fruit closer to the main stem are larger than those further away because they have access to current assimilates and NSC remobilised from the roots and wood (Singh *et al.* 2017).

### Contribution of sugars to reproductive development

Sugars play a key role in plant reproductive development by serving as fuel for cellular carbon and energy metabolism, while also acting as key signalling molecules (Rolland *et al.* 2006). The interplay between photosynthesis and NSC metabolism in source and sink organs generates diverse sugar signals that modulate reproductive processes. Starch mobilisation and the availability of sucrose emerge as crucial factors promoting flower induction and flowering. Additionally, the activity of invertases and the ensuing sugar metabolism contribute to reproductive processes, with hexoses playing a stimulatory role in the progression of both flower and fruit development (Ruan 2012).

#### Flowering

Flower induction is associated with the mobilisation of starch and an increase in leaf sugar export, which may also transport flowering-related hormones to the flowering bud (Rolland *et al.* 2006; Davenport 2009; Lauri and Normand 2017). Greater NSC content in terminal shoots corresponds

with heavier flowering (Pongsomboon *et al.* 1997). Flower abscission is also correlated with lower concentrations of sugars (Sawicki *et al.* 2015).

In mango, sugars produced in leaves are a potential driving force for phloem-based transport of a flowering promoter (Davenport 2007). The accumulation of NSC in the shoot apex is crucial for floral induction (Davenport 2009). The concentration of sucrose is highest in terminal and sub-terminal shoots at flowering, with roots, the trunk, stems and leaves exhibiting relatively lower concentrations (Normand *et al.* 2006). Higher concentrations of NSC or higher carbon-to-nitrogen ratio in a shoot increases the probability of flowering (Corbesier *et al.* 2002; Prasad *et al.* 2014).

Sucrose metabolism regulates flowering, along with T6P signals and gibberellins (Rolland *et al.* 2006; Sharma *et al.* 2019). Sucrose and its metabolising enzymes, notably sucrose phosphate synthase, appear to increase in leaves and terminal buds to trigger mango flowering, highlighting the important role of sucrose signalling to induce flowering (Prasad *et al.* 2014; Kaur *et al.* 2022). Increased supply of sucrose to the flowering shoot is also important for the emergence of panicles, while sucrose transporters are involved in determining flowering time (Liang *et al.* 2022). Moreover, the sucrose synthase signal associated with flowering may be mediated through T6P, as evidenced by its upregulation in the inflorescence (Kaur *et al.* 2022). TPS1 transcripts, involved in T6P synthesis, are expressed leading up to mango flowering, which could trigger T6P induced flower induction signals (Liang *et al.* 2022). Sucrose seems to function primarily in the leaf phloem to enhance the generation of florigens such as FLOWERING LOCUS T (FT), while T6P functions in the shoot apical meristem to promote the flowering signal pathway downstream of those florigens (Liang *et al.* 2022).

Horticultural practices aimed at manipulating flowering in mango trees, such as trunk or branch girdling and the application of plant growth regulators like ethephon and paclobutrazol, are closely linked to changes in NSC dynamics (Goren *et al.* 2003; Davenport 2007; Desta and Amare 2021). Girdling disrupts the phloem transport of sugars between the canopy and roots, offering a means to manipulate sugar distribution (Goren *et al.* 2003). In mango and other fruit trees, this manipulation, in turn, has the potential to reduce vegetative growth, induce flowering, and enhance fruit set and growth. Above the girdle, NSC accumulates, particularly in shoot terminals, leading to an improved carbon-to-nitrogen ratio and, consequently, enhanced flowering. Greater allocation of sugars to fruit following girdling also improves fruit size, dry matter and peel anthocyanin accumulation.

In lychee (*Litchi chinensis* L.), foliar application of the ethylene precursor, ethephon (2-chloroethylphosphonic acid), can suppress new vegetative growth before flower induction, promoting flowering (Cronje *et al.* 2022). Although less studied in mango, ethephon has shown promising flowering-inducing properties for the crop (Davenport 2009). In

lychee, ethephon induces bud dormancy, delays panicle emergence, and enhances flower development (Cronje *et al.* 2022). By inhibiting new growth and extending bud dormancy, ethephon prolongs the period for NSC reserve accumulation in terminal shoots, resulting in higher levels of starch and sugars at floral initiation, thereby contributing to improved flowering.

The triazole plant growth retardants, paclobutrazol and uniconazole, inhibitors of gibberellin biosynthesis, stimulate floral induction in mango (Davenport 2007; Rahim *et al.* 2011). By suppressing vegetative growth, they redirect sugars, originally available for vegetative growth, towards enhancing flowering, particularly through increased allocation to reproductive shoots (Yeshitela *et al.* 2004; Desta and Amare 2021).

### Fruit growth and retention

Fruit set in tree crops such as mango is regulated by the availability of sugars (Jannoyer and Lauri 2006). If flowering is heavy, sugar may limit the fruit set and growth causing the tree to rely more on NSC reserves (Chacko *et al.* 1982; Jannoyer and Lauri 2006).

Fruit abscission generally occurs during three stages: (1) shortly after fruit set; (2) mid-season; and (3) before harvest (Singh *et al.* 2004). Abscission after fruit set is due to poor fertilisation, hormonal signals and NSC related crosstalk, under high ethylene and low auxins (Singh *et al.* 2004; Xie *et al.* 2013; Sawicki *et al.* 2015). ABA also plays a key role in the initiation of an abscission layer. In contrast, high concentrations of gibberellins, cytokinins and auxins, are positively correlate with fruit retention (Singh *et al.* 2004; Xie *et al.* 2013). The availability of NSC is critical for fruit retention during later stages of development. Fruit and shoots may compete for NSC and accelerate abscission (Singh *et al.* 2004; Xie *et al.* 2013).

Hormones and sugars regulate abscission in plants (Sawicki *et al.* 2015). For example, in mandarin (*C. unshiu*), defoliation increases fruitlet abscission due to low sugar supply, an increase in ABA and ethylene, and a decrease in gibberellin (Gómez-Cadenas *et al.* 2000). Conversely, increased NSC supply decreases ethylene production and fruit abscission. Limited NSC supply to lychee fruitlets decreases auxin concentrations causing abscission (Kuang *et al.* 2012). In *Arabidopsis*, an overexpression of the T6P synthase gene *AtTPS1*, which regulates ABA signalling, occurs in abscising fruitlets (Avonce *et al.* 2004; Sawicki *et al.* 2015). Hence, T6P signalling may regulate ABA's stimulatory role in fruitlet abscission. Taken together, low sugar levels appear to reduce hormonal growth stimulants and increase stress signals, triggering abscission.

Research on the link between sugar, signalling and hormones in mango fruit retention is scarce. Sakhidin *et al.* (2011) found low sugar and high starch content predicted fruit abscission. This might be due to a reduction in starch metabolism in the pre-abscised fruit, allowing an accumulation of starch. Ethephon induces fruitlet abscission,

associated with an upregulation of ethylene receptors and a decrease in sucrose (Hagemann *et al.* 2015).

## Relationship between fruit and leaves

### Leaf-to-fruit ratio

Increased sink demand by developing fruit improves photosynthetic efficiency in crops (Aluko *et al.* 2021). For example, in peach (*Prunus persica* L.), DeJong (1986) showed  $A_{\text{net}}$  during early fruit development was similar in fruited and defruited trees. However, closer to fruit maturity,  $A_{\text{net}}$  was 11–15% higher in fruiting trees. Fruit increases  $A_{\text{max}}$  in mango and the concentration of nitrogen per leaf area (Urban *et al.* 2003).

Leaf  $A_{\text{net}}$  is affected by the leaf-to-fruit ratio (Urban *et al.* 2003, 2004a; Urban and Léchaudel 2005). A lower leaf-to-fruit ratio increases  $A_{\text{net}}$ , probably by exhausting NSC stored in the leaves (Urban *et al.* 2002). Partial defoliation of fruit trees increases photosynthesis in remaining leaves (Fischer *et al.* 2013; Pawar and Rana 2019). In contrast, a high leaf-to-fruit ratio increases leaf starch and inhibits photosynthesis (Urban *et al.* 2003, 2004a; Léchaudel *et al.* 2005a; Urban and Léchaudel 2005). Under low crop load, the accumulation of starch in leaves during the day reduces  $g_s$  and leaf nitrogen (Simmons *et al.* 1998; Urban *et al.* 2004a; Urban and Léchaudel 2005).

Accumulation of NSC in leaves under sink limitation, such as low crop load, may result in reduced TPU (Fabre *et al.* 2020), representing a limitation for  $A_{\text{max}}$  in mango (Urban *et al.* 2003). TPU signifies the rate at which triose phosphates are utilised for synthesising sugars and starch within leaves (Sharkey 2019; Zhou *et al.* 2023). Under sink limitation, NSC accumulate in leaves, and feedback inhibition on further sugar synthesis can inhibit TPU (Zhou *et al.* 2023), meaning TPU potentially modulates the influence of the leaf-to-fruit ratio on leaf source activity and sugar synthesis in mango.

### The proximity of fruit to the leaves

In terms of the relationships between reproductive development and photosynthesis, the proximity of fruit to leaves enhances or inhibits  $A_{\text{net}}$ , depending on the stage of fruit development (Shivashankara and Mathai 2000; Urban *et al.* 2004b). Flowering is associated with a decrease in  $A_{\text{net}}$  in leaves near inflorescences (Urban *et al.* 2004b, 2008). The reduction in photosynthesis is due to a decrease in electron flow in PSII,  $g_s$ , mesophyll conductance and  $J_{\text{max}}$ . A decrease in photorespiration may also contribute to lower  $A_{\text{net}}$  for leaves near flowers. Leaf nitrogen concentration is lower in leaves near inflorescences compared with leaves on vegetative shoots. Shivashankara and Mathai (2000) indicated that low  $A_{\text{net}}$  in flowering branches was due to lower carboxylation efficiency. After fruit set,  $A_{\text{max}}$  is positively related to the proximity of the leaves to fruit, independent of light and leaf age (Urban *et al.* 2003). This response is associated with

higher nitrogen concentration in leaves and a greater mass-to-area ratio rather than to NSC.

The contrasting effects of flowering and fruit growth on leaf nitrogen may be attributed to the availability of nitrogen at different stages of tree development. Total tree nitrogen content is lowest at flowering and increases after fruit set, especially in the leaves (Stassen *et al.* 2000). Flowering decreases leaf nitrogen due to the diversion of nitrogenous compounds from leaves to sinks such as the inflorescences (Durán-Zuazo *et al.* 2005). During fruit growth, the leaves and fruit accumulate nitrogen, indicating increased soil nitrogen uptake during this period (Stassen *et al.* 2000), suggesting that nitrogen is primarily directed towards the fruit and nearby leaves.

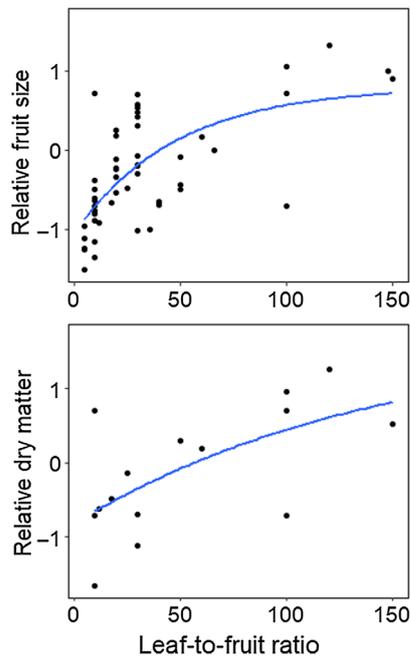
## Effect of crop load on reproductive development

High yields are important for profitability in mango cultivation. However, a heavy crop that draws on NSC reserves may reduce yield the following year. Depleted NSC reserves can lead to lower vegetative growth, resulting in less NSC accumulation to support production in the following year, thus, causing irregular bearing (Monselise and Goldschmidt 1982; Génard *et al.* 2008; Davenport 2009; Das *et al.* 2019). High yields are commonly achieved by improving harvest index, the ratio of yield-to-plant dry matter, rather than by improving photosynthesis (Génard *et al.* 2008). However, yield per land area is increased by enhancing leaf area and light interception (Menzel and Le Lagadec 2017).

### Fruit development

The effect of leaf-to-fruit ratio on mango fruit development is well investigated (Chacko *et al.* 1982; Reddy and Singh 1991; Simmons *et al.* 1998; Lechaudel *et al.* 2002; Léchaudel *et al.* 2005b; Urban and Léchaudel 2005; Léchaudel and Joas 2006; Léchaudel and Joas 2007; Grechi and Normand 2019). Typically, a shoot or branch with a set number of leaves and fruit was girdled to inhibit phloem translocation of sugars from external NSC sources. The results of these studies demonstrate that a low leaf-to-fruit ratio decreases the supply of NSC supply to the fruit. Fruit size and dry matter accumulation generally increase with the number of leaves per fruit (Fig. 4). It has been suggested that more than 30 to 50 leaves are required to support the growth of a single mango without support from reserves (Chacko *et al.* 1982; Reddy and Singh 1991).

In high cropping seasons or cultivars, there are often fewer than 30 leaves to support each fruit. Therefore, the balance between sources and sinks is maintained by NSC reserves (Fig. 1), which in turn is affected by the activities of the sources and sinks (Léchaudel *et al.* 2005a). Fruit set competes for limited NSC resources, and when flowering is heavy, the NSC may be inadequate for fruit set and growth (Jannoyer and Lauri 2006). Fruit retention is also affected, where ten leaves per fruit is inadequate (Grechi and Normand 2019).



**Fig. 4.** A logarithmic model for the meta-analysis of leaf-to-fruit ratio on fruit size (top) and fruit dry matter content (bottom) across regions, cultivars and tree ages. There was a significant exponential relationship for both fruit size (adj.  $R^2 = 44.2$ ) and dry matter content (adj.  $R^2 = 29.1$ ). Branches were girdled and either fruit or leaf removed. Data has been centred and scaled within each study and cultivar. Data for both trends has been drawn from Chacko *et al.* (1982); Simmons *et al.* (1998); Lechaudel *et al.* (2002); Léchaudel and Joas (2006) and Grechi and Normand (2019); and for fruit size from the additional studies: Reddy and Singh (1991); Urban and Léchaudel (2005) and Singh *et al.* (2007).

Pruning or fruit thinning can be used in orchards to manipulate source or sink size and alter fruit growth. Increasing the leaf-to-fruit ratio by fruit thinning results in larger fruit. In contrast, increasing the leaf-to-fruit ratio above 50 does not result in further increases in fruit size (Léchaudel *et al.* 2005a). Thus, when NSC limitations are removed, fruit growth is limited by the sink strength. When fruit size is not limited by the availability of NSC, excess carbohydrates are stored.

### Fruit composition

When the fruit are mature, sucrose concentration and starch hydrolysis correlate positively with an increasing leaf-to-fruit ratio. During ripening, a greater leaf-to-fruit ratio increases fruit respiration and the synthesis of the ethylene precursor, 1-aminocyclopropane-1-carboxylic acid (ACC) (Léchaudel and Joas 2006). A higher leaf-to-fruit ratio increases the accumulation of dry matter (Fig. 4) (Génard *et al.* 2008). In contrast, a low leaf-to-fruit ratio delays the degradation of starch to sucrose in mature fruit and increases glucose and fructose content on a dry mass basis (Léchaudel *et al.* 2005b; Léchaudel and Joas 2007).

NSC dynamics also contribute to physiological disorders in mango, particularly the development of spongy tissue disorder in mature fruit (Shivashankar and Sumathi 2019). This disorder, characterised by internal breakdown of mango flesh, is often observed in specific cultivars, including ‘Alphonso’ and ‘Tommy Atkins’. Fruit affected by spongy tissue disorder exhibit lower amylase activity and sugars during ripening, whilst having higher starch content compared to healthy fruit. Increased competition for resources, such as NSC, among developing fruits for seed development is believed to play a crucial role in the occurrence of spongy tissue disorder (Shivashankar and Sumathi 2019). Consequently, amylase activity is reduced, and starch degradation is impeded in affected fruit.

### Reserves and storage organs

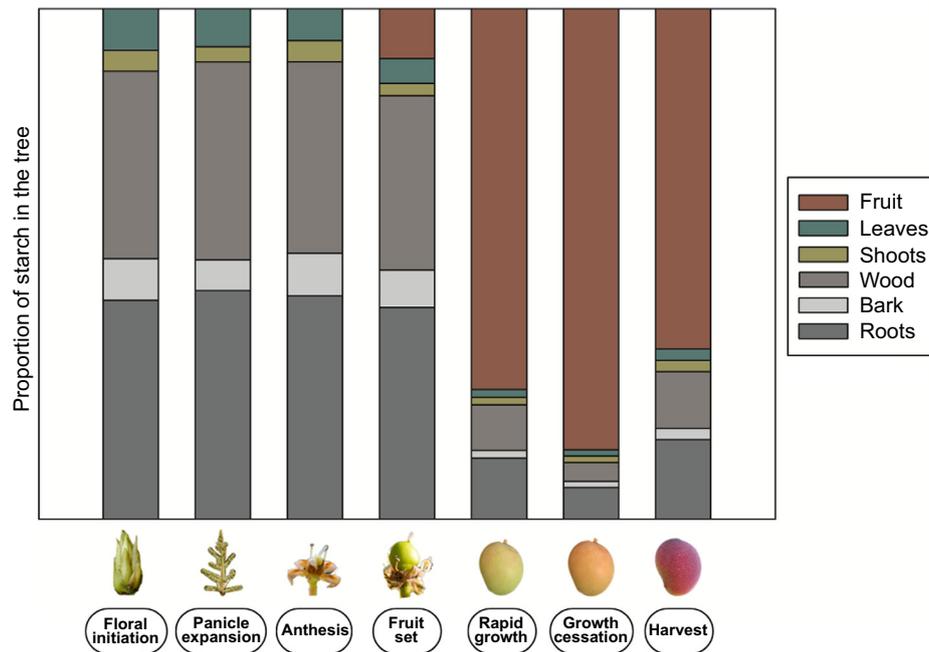
Roots, trunks, branches and shoots predominantly function as sinks. Nevertheless, some organs undergo transitions from sinks to sources, such as roots and stems, which can transiently shift from storage sinks to sources (Sonnewald and Fernie 2018). The storage organs serve as energy reserves for future growth and development.

In mango, the fruit represents the principle sink and hence, secondary NSC sinks accumulate starch only when the fruit sink strength declines or is absent (Stassen and Janse van Vuuren 1997; Davie *et al.* 1999) (Fig. 5). The concentration of starch in vegetative tissues increases through bud development and peaks prior to flowering (Davie *et al.* 1999; Normand *et al.* 2006). The majority of the starch is stored in thick roots and woody tissues, mainly roots larger than 10 mm in diameter and branches (Stassen and Janse van Vuuren 1997; Normand *et al.* 2009). Smaller contributions arise from bark, thin roots, scaffolding branches, shoots and terminal growth units.

### Remobilisation

The development of evergreen trees relies on current photoassimilates as the primary source of NSC (Olesen *et al.* 2008). However, reserves can buffer against fluctuations in the supply of current photosynthates (Fig. 1). During elevated photosynthate production, branches are primarily self-supporting (Sprugel *et al.* 1991). However, when the leaf area is reduced or sink demand is amplified, strong sinks can draw NSC from outside the branch. Root starch reserves are the first utilised for fruit development prior to the remobilisation of starch stored in woody tissues (Davie and Stassen 1997b). In fruiting species, remobilisation from storage tissues occurs when sink requirements exceed source production (Loescher *et al.* 1990; Candolfi-Vasconcelos *et al.* 1994; Han *et al.* 2016; Rossouw *et al.* 2017b; Breen *et al.* 2020).

Roots and woody tissues such as the trunk, branches, bark and shoots act as sources rather than sinks during flowering,



**Fig. 5.** Theoretical changes in distribution of starch from floral bud initiation to harvest in roots, bark, wood, shoots, leaves and fruit in mango. Inspired by [Stassen and Janse van Vuuren \(1997\)](#); [Davie \*et al.\* \(1999\)](#) and [Normand \*et al.\* \(2006\)](#).

spring vegetative growth flush, fruit set and fruit growth when their starch is depleted ([Stassen and Janse van Vuuren 1997](#); [Davie \*et al.\* 1999](#)). The demand for NSC exceeds the current supply from photosynthesis, resulting in the mobilisation of reserves. At flowering, roots contain higher concentrations of starch than other vegetative tissues, particularly coarse roots, the taproot and stump ([Normand \*et al.\* 2006](#)). Medium roots (2–10 mm in diameter), the trunk, branches and older leaves have intermediate starch levels, whereas fine roots (<2 mm in diameter) and terminal and subterminal growth units of shoots have the lowest starch levels.

### Effects of fruiting on reserves

The impact of fruiting on NSC and on vegetative and reproductive development have been extensively studied in deciduous fruit crops ([Holzapfel \*et al.\* 2010](#); [Fischer \*et al.\* 2013](#); [Rossouw \*et al.\* 2017b](#)). However, research in this area is scarce for evergreen species such as mango. Intra-annual variation in NSC concentration might not vary to the same extent as in deciduous species. However, there is still cycles due to seasonal and phenological changes in evergreen species ([Normand \*et al.\* 2006](#)).

In grapevine, a high yield leads to a depletion of starch reserves at harvest ([Rossouw \*et al.\* 2017a](#)). This results in lower yields in the following season ([Smith and Holzapfel 2009](#)). In contrast, when apple trees were defoliated causing NSC reserves to deplete, the yield for the next season was unaffected ([Breen \*et al.\* 2020](#)). The role of NSC reserves in

inter-annual yields varies amongst deciduous species and between deciduous and evergreen species.

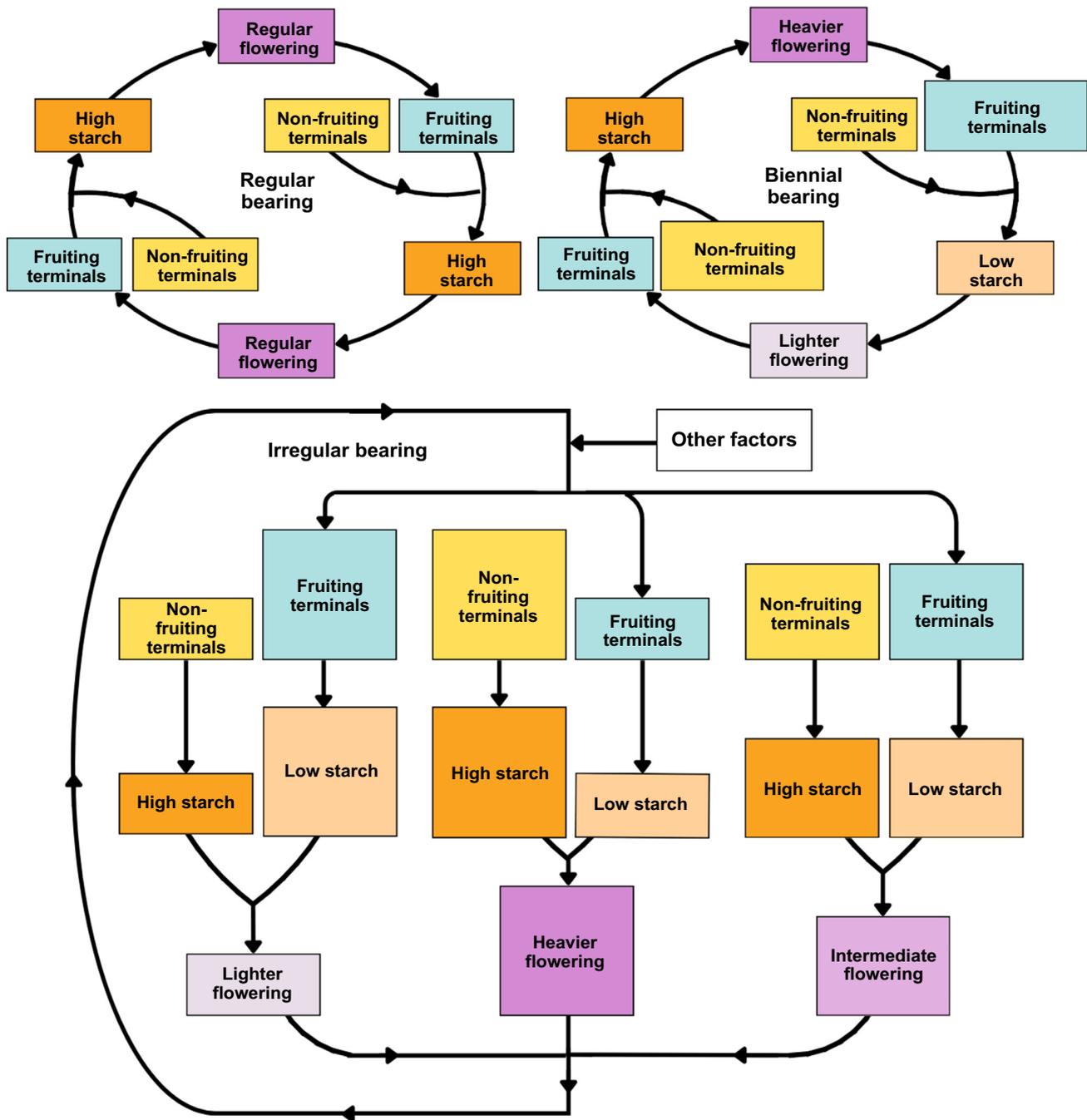
The importance of reserves for reproductive growth in deciduous crops depends on the timing of flowering and fruit development ([Loescher \*et al.\* 1990](#)). If flowering occurs before the canopy is formed, there is greater reliance on reserves for fruiting. However, yield also influences the role of NSC reserves as they are necessary to balance source production and sink demand.

### Bearing pattern

Biennial or alternate, and irregular bearing occurs in mango and are influenced by the cultivar, agronomic practices, and the environment ([Shivashankara and Mathai 2000](#); [Sharma \*et al.\* 2020](#)). These phenomena all contribute to low productivity ([Pandey 1989](#)). Irregular bearing is characterised by an irregular pattern of fruiting across different seasons ([Smith and Samach 2013](#); [Sharma \*et al.\* 2019](#)) (Fig. 6). In biennial bearing, a heavy yield is followed by a light yield in the following year ([Sharma \*et al.\* 2019](#)). ‘Off’ and ‘on’ years are often associated with cycles of carbohydrate reserves (Fig. 6).

### Links between bearing pattern and NSC

Reserve NSC concentrations can limit flower and fruit development ([Whiley \*et al.\* 1989](#); [Normand \*et al.\* 2006](#)), as high NSC at fruit bud differentiation is positively correlated



**Fig. 6.** Starch regulation in fruiting and non-fruiting terminal shoots contributes to the distinctive flowering patterns in regular (top left), biennial (top right), and irregular bearing (bottom) mango cultivars. Larger box size corresponds with a greater proportion. Regular bearers maintain high starch concentrations in both previously fruiting and non-fruiting terminals, ensuring consistent flowering and fruiting cycles. Biennial bearers, experiencing seasons of abundant flowering, exhibit reduced terminal starch levels in subsequent cycles, resulting in poor flowering before recovery. Irregular bearers display a less predictable pattern, with previously fruiting terminals having lower starch and previously non-fruiting terminals having higher starch in the next cycle. The balance between these terminal types, along with factors like abiotic conditions, influences the irregular bearing pattern.

with yield in mango. A high yield provides a strong sink for NSC, limiting flowering the following season (Chacko *et al.* 1982; Fischer *et al.* 2013; Sharma *et al.* 2019). Limited vegetative growth also results from low NSC and reduces

the number of terminal growth units that can flower (Normand *et al.* 2017). Low NSC limits fruit set and development resulting in biennial or irregular bearing (Davie and Stassen 1997b).

Yields across different seasons are related to the availability and replenishment of starch reserves (Reddy and Singh 1991; Capelli *et al.* 2021). High starch levels in the leaves and stems are correlated with better flowering and yields (Suryanarayana 1978; Monselise and Goldschmidt 1982). Branch terminals have low concentrations of starch after harvest, and starch accumulation is slower in fruiting terminals than quiescent and flowering terminals (Normand *et al.* 2017). Vegetative flushing after harvest further depletes starch accumulation (Capelli *et al.* 2021). In contrast, in non-fruiting growth units, starch accumulates after harvest. This is why previously fruiting growth units are less likely to have timely vegetative growth. Decreased vegetative growth, in turn, limits flowering and fruiting in the following cycle.

### Differences amongst cultivars

Irregular bearing cultivars have high fluctuations in yield over different seasons and are highly influenced by abiotic factors such as temperature and water supply (Sharma *et al.* 2019) (Fig. 6). In contrast, biennial bearing cultivars have an on-and-off yields (Fig. 6). Das *et al.* (2019) and Capelli *et al.* (2021) found that irregular and biennial bearing cultivars differ in their storage and use of starch. Differences in starch between fruiting and non-fruiting terminals are greater in irregular ‘Cogshall’ than in biennial ‘José’ after harvest (Capelli *et al.* 2021). In regular ‘Amrapali’, buds and leaves had higher NSC than biennial ‘Dashehari’ (Das *et al.* 2019). In previously fruiting growth units on irregular bearing cultivars, low starch reduced vegetative growth compared with previously non-fruiting growth units. The proportion of non-fruiting growth units across the canopy dictates growth and potential flowering. This information can help guide canopy management in mango orchards. The key is to achieve a balance of fruiting and non-fruiting growth. Selective pruning can remove some of the fruiting terminals, providing a better balance between fruiting and non-fruiting terminals.

For biennial bearers, low starch in fruiting and non-fruiting terminals decrease vegetative growth. All terminals behave similarly leading to poor vegetative growth and flowering. Regular bearers maintain a balanced concentration of NSC each season, whereas biennial bearers have wide fluctuations in NSC concentration. In ‘on’ seasons, NSC levels drop for the biennial bearer, and in the ‘off’ season the biennial bearer exhibits lower reserves (Sharma *et al.* 2020).

Additionally, the number of leaves required to support a single fruit is higher in the biennial ‘Dashehari’ and ‘Langra’ compared with the consistent ‘Neelum’ and ‘Kalahandi’ (Reddy and Singh 1991). This response could be due to differences in fruit size, leaf area and photosynthesis. Lastly, rootstock selection could alter the bearing habit of scion cultivars by influencing the carbon-to-nitrogen ratio in buds (Vittal *et al.* 2023). For biennial ‘Dashehari’, the rootstock Kurukkan was able to improve the carbon-to-nitrogen ratio

in buds as compared to another rootstock, Olour. A higher carbon-to-nitrogen ratio is conducive to flowering and may help reduce erratic bearing.

### Conclusions

Starch–sugar metabolism regulates carbon allocation in fruit trees. Starch reserves in roots and wood are synthesised when sugars are abundant or degraded upon sugar starvation. The availability of starch reserves influences flowering, fruit set, and growth, with the inability to recover starch post-harvest leading to irregular bearing.

Sugars function as a mobile energy source and in signalling with phytohormones to stimulate floral induction, and fruit set, retention and growth. Sucrose signals modulate fruit development by regulating starch metabolism, maintaining cellular carbon homeostasis, while T6P is a potent signalling molecule to balance NSC supply with demand. In later fruit development, sugar-phytohormone cues regulate the accumulation of pigments such as anthocyanins and carotenoids in peels.

Fruit is the major NSC sink whereas leaves are the major source. When yields are low, leaf starch accumulates, leading to reduced photosynthesis. Conversely, high yields deplete leaf starch, and stimulates photosynthesis. Photosynthesis negatively correlates with the proximity of inflorescences to leaves during flowering, and positively correlates with the proximity of leaves to growing fruit.

Leaf activity peaks when fruit are approximately half to fully grown, corresponding to fruit sink demand. However, leaf NSC supply often falls short, necessitating the remobilisation of reserves. Larger roots, trunk, and branches store starch reserves, crucial for reproductive development, including flowering, fruit set, growth, and dry matter accumulation. These reserves are replenished when fruit activity declines. Insufficient photosynthate and starch storage lead to reduced fruit size and dry matter accumulation, impacting long-term productivity when crop load is excessive. Crop load management techniques, for instance, crop thinning, commonly used in temperate crops, could be considered for mango in high crop load years. This approach could help prevent the depletion of NSC reserves, potentially leading to more consistent bearing across seasons.

This review identifies various gaps in understanding the effects of NSC on fruiting and mango productivity. Exploring sugar signalling under a range of NSC availabilities, particularly T6P signalling, and investigating interactions between sugars, phytohormones and secondary metabolites during flowering and fruit development are crucial. Developing a carbon balance, considering the effects of crop load on NSC reserves and carbon assimilation in mango leaves, is essential. An improved understanding of NSC autonomy in terms of proximal and distal sources and their

recharge during and after fruiting will contribute to managing irregular bearing effectively.

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