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SPECIAL ISSUE ARTICLE

Carbon fluxes and environmental interactions during legume development, with a specific focus on *Pisum sativum*

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Abstract

Grain legumes are major food crops cultivated worldwide for their seeds with high nutritional content. To answer the growing concern about food safety and protein autonomy, legume cultivation must increase in the coming years. In parallel, current agricultural practices are facing environmental challenges, including global temperature increase and more frequent and severe episodes of drought stress. Crop yield directly relies on carbon allocation and is particularly affected by these global changes. We review the current knowledge on source-sink relationships and carbon resource allocation at all developmental stages, from germination to vegetative growth and seed production in grain legumes, focusing on pea (*Pisum sativum*). We also discuss how these source-sink relationships and carbon fluxes are influenced by biotic and abiotic factors. Major agronomic traits, including seed yield and quality, are particularly impacted by drought, temperatures, salinity, waterlogging, or pathogens and can be improved through the promotion of beneficial soil microorganisms or through optimized plant carbon resource allocation. Altogether, our review highlights the need for a better understanding of the cellular and molecular mechanisms regulating carbon fluxes from source leaves to sink organs, roots, and seeds. These advancements will further improve our understanding of yield stability and stress tolerance and contribute to the selection of climate-resilient crops.

1 | INTRODUCTION

Legumes have been consumed for millennia and remain a staple food cultivated worldwide for their high nutritional value. Rich in proteins and starch, legumes make an essential food for human diet and animal forage. In this review, we mainly focus on the pea crop (*Pisum sativum*), which is particularly rich in various nutrients, notably proteins. Its seeds contain starch (50%), proteins (25%), soluble sugars (5%), fibers (5%), and also vitamins and minerals (Bastianelli et al., 1998). Plant-based proteins are a promising alternative to meat consumption and could reduce the global impact of food production on the environment (Sandberg, 2011). As a result, the international market for pea proteins is booming and opportunities are rising for the market of starch valorization (Yu et al., 2021). This societal challenge towards more

sustainable practices in the context of global environmental changes implies a reconsideration of the current agricultural system.

The yield of many crops rarely reaches its maximum potential of production. This is particularly the case for grain legumes which have benefited from fewer agronomic improvement programs than cereals (Foyer et al., 2016). For instance, yields of wheat in France increased on average by 92 kg ha⁻¹ year⁻¹ between 1961 and 2018, while those for pea only increased by 37 kg ha⁻¹ year⁻¹ over the same period (FAOSTAT, 2021). This large difference is in part attributable to unfavorable environmental conditions. Indeed, grain legume production is particularly affected by environmental factors, both biotic and abiotic, causing an unstable production with large variability in yield (Bénézit et al., 2017; Smith et al., 2018). Several stresses negatively impact plant production but drought, temperatures, salinity, and

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waterlogging are the major abiotic stresses implicated in crop yield destabilization (Rane et al., 2021; Zander et al., 2016). Drought stress is the main constraint that affects crop yield and quality. A low water availability associated with high temperatures can also result in higher soil salt concentration (Rane et al., 2021; Saberi Riseh et al., 2021). Moreover, because of climate change, dry periods alternate with wet episodes leading to waterlogging and submergence of the aerial part (Rane et al., 2021). Global climate change, associated with a degrading environment, amplifies these major stresses, impacting crop development, and productivity. Developing new crop varieties more resilient to climate change and ensuring yield stability to feed the world's growing population, while complying with environmental sustainability, represent a huge challenge (Dhankher & Foyer, 2018; Martignago et al., 2020; Smith et al., 2018). To this end, breeders and researchers must focus on understanding how the environment influences yields in crops (Bénézit et al., 2017; Smith et al., 2018; Strydhorst et al., 2015).

Crop yield directly relies on carbon fluxes, which is particularly affected by global changes. To counteract the effects of environmental stresses, a significant part of the energy captured by photosynthesis is redirected, which generates yield losses. Indeed, in optimal conditions, the carbon fixed by photosynthesis will be primarily allocated towards sink organs (roots, young leaves, flowers, pods, and seeds), also mediating a flow of nitrogenous substances to these organs. Altogether, this contributes to the optimal nutritional filling of carbon (starch) and nitrogen (proteins) into seeds. Conversely, if the plant is subjected to biotic or abiotic stresses, a significant part of the carbon will be diverted, and thereby lost for sink organs (Chen et al., 2006; Durand et al., 2016; Fougereux et al., 1997; Guilioni et al., 1997; Henriot et al., 2019). A better understanding of the modulation of these carbon fluxes during both biotic and abiotic stresses and uncovering the genes involved in these biological processes will contribute to improving legume productivity.

Carbon fluxes are mediated by sugar transport proteins of the SUCROSE TRANSPORTER (SUT), MONOSACCHARIDE TRANSPORTER (MST), and SWEET (SUGARS WILL EVENTUALLY BE EXPORTED TRANSPORTER) families. Notably, SUTs, MSTs, and SWEETs control the loading of photosynthates from source leaves and coordinate carbon fluxes towards sink organs (e.g., root and seed), thereby determining the yield and nutritional quality of seed crops (Sosso et al., 2015). Their crucial roles in response to environmental factors have also been highlighted in model crops (Lemoine et al., 2013), but their contribution to stress tolerance has been overlooked in legumes. In addition, sugar transport and carbon metabolism genes have potential applications as biomarkers in plant breeding programs (Schroeder et al., 2013; Sosso et al., 2015; Wang et al., 2008). Today, pea enters the genomic era with a reference genome recently sequenced (Kreplak et al., 2019). This represents a major advance and should help identify genetic markers for yield and stress tolerance in pea. We recently identified major genes mediating sugar transport (*PsSUT*, *PsMST*, and *PsSWEET*) and carbon metabolism genes (*PsINV*) in *P. sativum*, focusing on plant productivity in response to drought (Doidy et al., 2019; Morin et al., 2022).

Here, we review major research advances on carbon partitioning in grain legumes, with a specific focus on pea crop and in response to environmental challenges. We cover the properties and processes governing carbon allocation and sugar transport during legume development, from germination to seed production. We also highlight current knowledge on the biological pathways at the molecular level and propose hypotheses to improve the resilience of legume crops towards major environmental changes.

2 | CARBON FLUXES DURING SEED GERMINATION AND SEEDLING ESTABLISHMENT

Germination is a key developmental process including imbibition and metabolism recovery of the seed resulting in the emergence of the root and the shoot (Figure 1A). Dry pea storage compounds mainly consist of starch, proteins, soluble sugars, and fibers. The most abundant soluble sugars in dry pea seeds are sucrose and RFOs, mainly stachyose and verbascose (Kuo et al., 1988; Vidal-Valverde et al., 2002). To sustain growth and seedling establishment, these reserves must be remobilized. The role of RFOs catabolism during early pea germination has been highlighted by a 25% decrease in the germination rates when α -galactosidase was chemically inhibited (Blöchl et al., 2007). Degradation of RFOs leads to an increase in sucrose, glucose, and fructose (Vidal-Valverde et al., 2002), and when the radicle emerges, 50% of the RFOs are already metabolized. Starch remobilization occurs later on as amylase activity is enhanced between 4 and 10 days after imbibition (Yomo & Varner, 1973). Pea storage compounds are degraded and transported from the cotyledons to the embryo axis to be directed to the root and the shoot (Figure 3). In germinating pea seeds, several *SUTs*, *SWEETs*, and *CWINVs* (cell wall invertases) genes are strongly expressed in the first days following imbibition (Jameson et al., 2016). For instance, the authors showed a strong induction of *PsSUT3* (renamed¹ *PsSUT2*), *PsSWEET12* and *PsCWINV6* (renamed *PsCWINV2.1*) after 4 h of imbibition. This suggests a transport of hexoses and sucrose from the cotyledons to the growing sink organs during the germination process (Figures 1A and 3). Indeed, cotyledons are the major source organs at the beginning of seedling development. By removing one cotyledon (source organ) or by manipulating the sink strength by adding sucrose, Schulz (1994) showed that the translocation of sugars is sink-regulated in pea seedlings, mainly through the apical root region (Schulz, 1994). The main gene that seems involved in sugar translocation is *PsSUT1* (renamed *PsSUT1.1*) (Figure 3), which is strongly expressed in shoot and root (Jameson et al., 2016). This demonstrates that source-sink relationships are rapidly established after imbibition (Figure 1A) and subsequent degradation of the cotyledon storage compounds is linked to a transition from germination and seed reserve dependency to autotrophy and sugar production through photosynthesis.

During their development, crops must face various abiotic stresses (Figure 1A). Major stresses include drought stress,

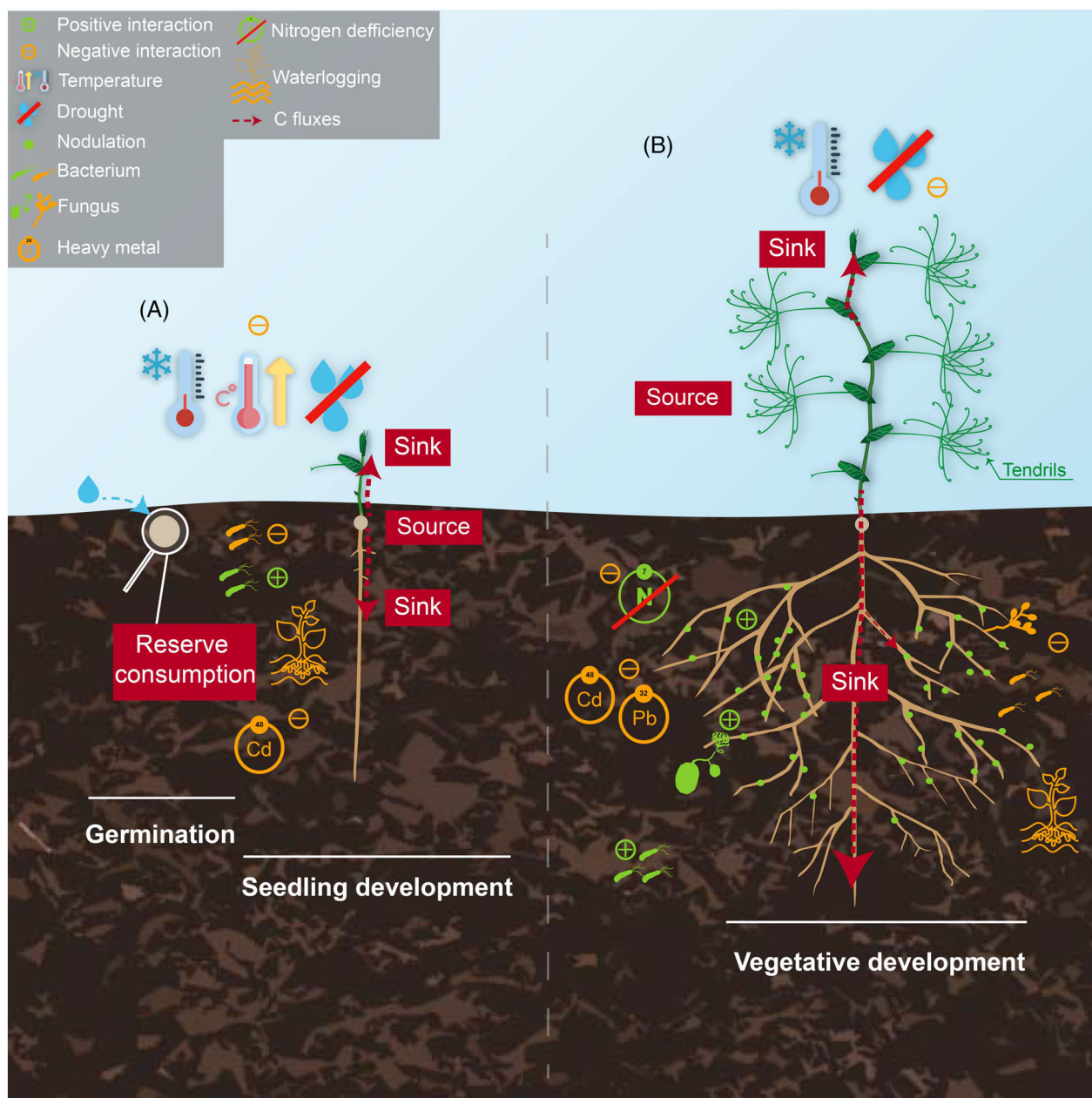


FIGURE 1 Schematic representation of carbon fluxes during germination, seedling development and vegetative development of pea, influenced by beneficial (green) or detrimental (yellow) environmental factors. During germination and seedling development (A), cotyledons are the main source organs, and their growth is dependent both on temperature and water availability. Abiotic factors indeed enhance or diminish germination and seedling elongation rates. During vegetative development (B), leaves provide sugars mainly to the root system, especially to the taproot. This trophic relationship can be favored by beneficial microorganisms or diverted by pathogens. Afterwards, the main source organs are mature leaves which provide sugars to the root system and the apical meristem. Biomass production is increased by beneficial microorganisms (N-fixing bacteria, mycorrhiza, and PGPR), which can help the plant to cope with mineral deficiency and other abiotic and biotic stresses. At this developmental stage, pea plants often face cold temperatures and drought. Pathogens such as fungi, nematodes, or bacteria, also divert carbon fluxes for their benefit. Altogether, these stresses affect growth and thereafter seed production

temperature, salinity, and waterlogging. In pea, germination and seedling establishment are sensitive to thermic stress, which affects seed germination rate. Even though pea seeds are rather highly tolerant to cold and can germinate on ice (Macherel et al., 2007), germination rates tend to increase with temperatures, reaching an optimum between 21°C and 27°C (Raveneau et al., 2011). These optimal

temperatures probably allow a better activity of the hydrolytic enzymes and sugar transporters into the cotyledons. Water deficit also affects germination (Figure 1A) (Raveneau et al., 2011) (Table 1). By adding PEG to germinating seeds, germination percentages in three pea varieties were dramatically reduced from 100% to 5% at an osmotic potential of -0.8 MPa (Okçu et al., 2005) (Table 1).

TABLE 1 Overview of the main results on pea responses to challenging environments

Stress	Developmental phase	Experimental results	Reference
Abiotic stress			
Cadmium	Seed germination	Probable inhibition of sucrose transport	Devi et al. (2007)
	Vegetative stage	Lower chlorophyll content with subsequent reduced photosynthesis	Sandalio et al. (2001)
Cold	Seed germination	Suboptimal activity of hydrolytic enzymes reducing germination rates	Raveneau et al. (2011)
	Vegetative stage	Increased leaf and root soluble sugars levels/ temporary starch storage to compensate for loss of photosynthetic activity in a pea winter variety	Bourion et al. (2003)
Drought	Seedling stage	Accumulation of carbohydrates and proteins	Al-Quuran et al. (2021)
	Vegetative stage	Osmotic adjustment through soluble sugar accumulation in leaves	Kumar et al. (2021), Lahuta et al. (2022), Sanchez et al. (1998, 2004)
	Vegetative stage	Increased osmotic potential in roots	Kumar et al. (2021), Lahuta et al. (2022)
	Vegetative stage	Increased content of sucrose, glucose, and sugar alcohol in the phloem sap	Blichartz et al. (2021)
	Flowering stage	Decrease of plant biomass	Prudent et al. (2016)
	Flowering stage	Decrease of flower and pod number	Nadeem et al. (2019)
	Seed development	Reduction in individual seed weight and seed number	Ney et al. (1993), Guillioni et al. (2003), Nadeem et al. (2019)
	Flowering stage	Cessation of reproductive organ formation and subsequent flower abortion	Guillioni et al. (1997)
Heat stress	Flowering stage	Cessation of reproductive organ formation and subsequent flower abortion	Guillioni et al. (1997)
Osmotic stress	Seed germination	Decrease of germination percentages	Okçu et al. (2005)
Waterlogging	Vegetative stage	ROS production, reduced plant growth, and seed yield	Pampana et al. (2016a), Rane et al. (2021)
Pathogens			
<i>Rhodococcus fascians</i>	Seed germination	Changes in source-sink relationship between cotyledons and shoot/root	Dhandapani et al. (2017)
<i>Erysiphe pisi</i>	Vegetative stage	Increased invertase enzyme activity	Storr and Hall. (1992)
<i>Erysiphe pisi</i>	Vegetative stage	Promotion of resistance through overexpression of <i>MtSTP13.1</i>	Gupta et al. (2021a, 2021b)
Ascochyta blight (not specified)	Seed development	Yield loss	Bretag et al. (1995)
<i>Mycosphaerella pinodes</i>	Seed development	Decreased seed starch content	Garry et al. (1996)

Moreover, seedlings grown under different soil water holding capacities contained more proteins and carbohydrates, with a proportional increase related to the stress intensity (AL-Quraan et al., 2021) (Table 1). Sucrose accumulation is a common response of seedlings to dehydration, probably thanks to the increased activity of sucrose synthase. During water stress, sucrose content increases earlier and is higher in pea roots than in epicotyls (but not in cotyledons) and these changes are associated with a lower accumulation of galactinol and raffinose (Lahuta et al., 2014). This accumulation of carbohydrates could enable seedlings to maintain a low water potential, therefore, promoting water uptake to cope with water deficit. In the field, a dry period may be followed by strong rainfall leading to a waterlogging episode (Figure 1A). This stress inhibits cellular aerobic respiration and induces anoxic soil conditions that can increase the concentrations of toxic compounds (Pampana et al., 2016a, 2016b; Rane et al., 2021). Heavy metals, such as lead (Mittal & Sawhney, 1990) and cadmium (Devi et al., 2007), can affect pea seed germination (Figure 1A). The

addition of cadmium resulted in decreased α - and β -amylase activities leading to a reduction of starch degradation in cotyledons (Devi et al., 2007). However, sucrose synthesis was not affected in source cotyledons, but the sucrose content was modified in the sink radicle and shoot. The negative effect of cadmium could therefore mainly be due to an inhibition of sucrose transport (Table 1). This could be linked to seedling growth reduction as well as variations in carbohydrate composition (Devi et al., 2007).

In addition to abiotic constraints, pathogenic microorganisms can also be detrimental for pea germination and early seedling growth (Figure 1A). Indeed, pea is sensitive to several pathogens, and this from the start of its lifecycle. For instance, inoculation of a pathogenic strain of *Rhodococcus fascians* on germinated pea plants resulted in reduced root growth and multiple shoot formation with intact cotyledons (Dhandapani et al., 2017). In cotyledons, the expression of *PsSWEET*, *PsSUT*, and *PsINV* genes was higher than in the noninfected control, suggesting changes in the source-sink relationship induced by the

pathogen, with cotyledons maintained as sinks for its benefit rather than evolving to a source tissue sustaining plant growth (Table 1).

Altogether, data in the literature point to a strong dependency between seed sugar remobilization for seedling development and their adaptation to environmental constraints. When the seedling's environment enables its establishment, vegetative development proceeds and source-sink relationships evolve, with mature leaves becoming the main source organs.

3 | CARBON FLUXES IN SHOOT DURING VEGETATIVE DEVELOPMENT

3.1 | Sugar fluxes and signals for axillary bud growth

Pea plants have an indeterminate growth habit with the successive addition of phytomers defining the main stem. At each node, an axillary bud has the capacity to develop in a lateral branch, according to the same scheme as the main axis. Lateral branches will support the growth of more flowers and pods. Therefore, the number of lateral branches will have a positive impact on yield (Patrick & Colyvas, 2014). In pea, lateral branches are usually located on the lowest vegetative nodes (Doré, 1994) but growing conditions and genotype can affect the number and position of branches. However, the number of axillary branches depends heavily on photosynthate (mainly sucrose) availability (Patrick & Colyvas, 2014). Pea has been a model for studying branching, allowing the discovery of the role of auxin, cytokinins, and more recently strigolactones in the release of apical dominance (for review see Rameau et al., 2015). The role of sucrose as an antagonist of auxin on axillary bud outgrowth has been described in the past decade. In pea, Mason et al. (2014) demonstrated that sucrose is “both necessary and sufficient” for the initial release of axillary buds from apical dominance before the auxin concentration in the bud is affected. This initial effect could of course be linked to the trophic role of sucrose; however, it was also possible to induce a similar rapid release of bud growth with nonmetabolized analogs of sucrose. Thus, Barbier et al. (2015) suggested that sucrose is also involved in a signaling pathway. However, hexoses derived from sucrose may also be involved considering the recently discovered role of HEXOKINASE 1 (HXK1) in regulating shoot branching (including in pea; Barbier et al., 2021). Bertheloot et al. (2020) proposed a quantitative model for the interactions of sucrose with the hormonal pathways regulating bud outgrowth. This model, in rose and in pea, suggests that plant sugar status modulates the auxin-controlled apical dominance. This latter can be maintained only if the sugar status of the plant is low. On the opposite, if the plant's sugar status is high, apical dominance is low and axillary buds develop with, in the case of pea, a positive effect on yield as mentioned above. The link between the sugar status of the plant and the development of axillary buds may represent an adaptative response to the environment (Bertheloot et al., 2020).

Trehalose-6-phosphate (Tre6P), a sugar signaling molecule, has recently been implicated in shoot branching in *Arabidopsis* (Fichtner &

Lunn, 2021). Increasing the level of Tre6P in the vasculature had a positive effect on branching. Interestingly, the expression of the sucrose transporter genes *AtSWEET11* and *AtSWEET12* was also increased. In *Rosa hybrida*, *RhSUC2* expression was increased, together with an influx of sucrose, in the bud during bud burst (Henry et al., 2011). In *Chrysanthemum morifolium*, *CmSWEET17* expression was increased during bud outgrowth, and its overexpression promoted bud growth (Liu et al., 2020). Taken together, these results indicate that increased expression of sucrose transporter genes is associated with an increased flux of sucrose towards the bud, thus promoting bud outgrowth.

3.2 | Carbon fluxes in source leaves

Pea leaves are pinnate and are composed of a basal pair of stipules, 2–3 pairs of basal leaflets and a terminal tendrils. In pea, a wide variety of genotypes are available, some carrying mutations leading to different arrangements of the leaf parts. The most described is the *afila* mutation, where all leaflets are replaced by tendrils (Figure 1B). The leaf is therefore reduced to a pair of basal stipules and distal pairs of tendrils that are branched, forming together the tendrils complex (Côté et al., 1992a). In conventional (*leafy*) cultivars, it was assumed that the contribution of tendrils was neglectable. However, it has been demonstrated that mature tendrils act as source organs and export photo-assimilates through the phloem (Côté et al., 1992a). Further studies by Côté et al. (1992a) specified that the sink/source transition occurs when tendrils begin to coil. The authors calculated that 65%–70% of the carbon gained per day can be attributed to the tendrils in an *afila* genotype (Côté et al., 1992b).

Little is known about sugar transport at the molecular level in different pea genotypes. In *Arabidopsis*, it is commonly accepted that sucrose is transported from the mesophyll cells, where it is produced, to the phloem parenchyma cells through symplastic transport (Lalonde et al., 2003) (Figure 3). Sucrose is then unloaded into the apoplasm near the conductor complex (companion cell/sieve element) by two facilitators: *AtSWEET11* and *AtSWEET12* (Chen et al., 2012) (Figure 3). As sucrose concentration of the conducting complex is much higher than in the apoplast, the influx of sucrose requires active transport by the sucrose transporter *AtSUC2* (Ayre, 2011; Dinant & Lemoine, 2010; Lalonde et al., 2004). *P. sativum* also seems to possess a similar phloem loading configuration (Van Bel & Gamalei, 1992). Therefore, we could postulate that *PsSWEET12* (*AtSWEET12* homolog) mediates the efflux of sucrose into the apoplasm, while *PsSUT1.1* (*AtSUC2* ortholog) is responsible for loading sucrose into the phloem (Doidy et al., 2019) (Figure 3). Ninan et al. (2019) studied the expression of *PsSUT* and *PsCWINV* genes during leaf development and senescence in two cultivars: Bolero (*leafy*) and Bohatyr (*afila*). *PsSUT1* (renamed *PsSUT1.1*) and *PsSUT2* (renamed *PsSUT1.4*) were identified as the most expressed *SUT* genes, both in mature and senescent leaves (Figure 3), but with a lower expression in leaves of the Bolero cultivar. However, the authors did not investigate the different parts (stipules, leaflets, tendrils) independently. In

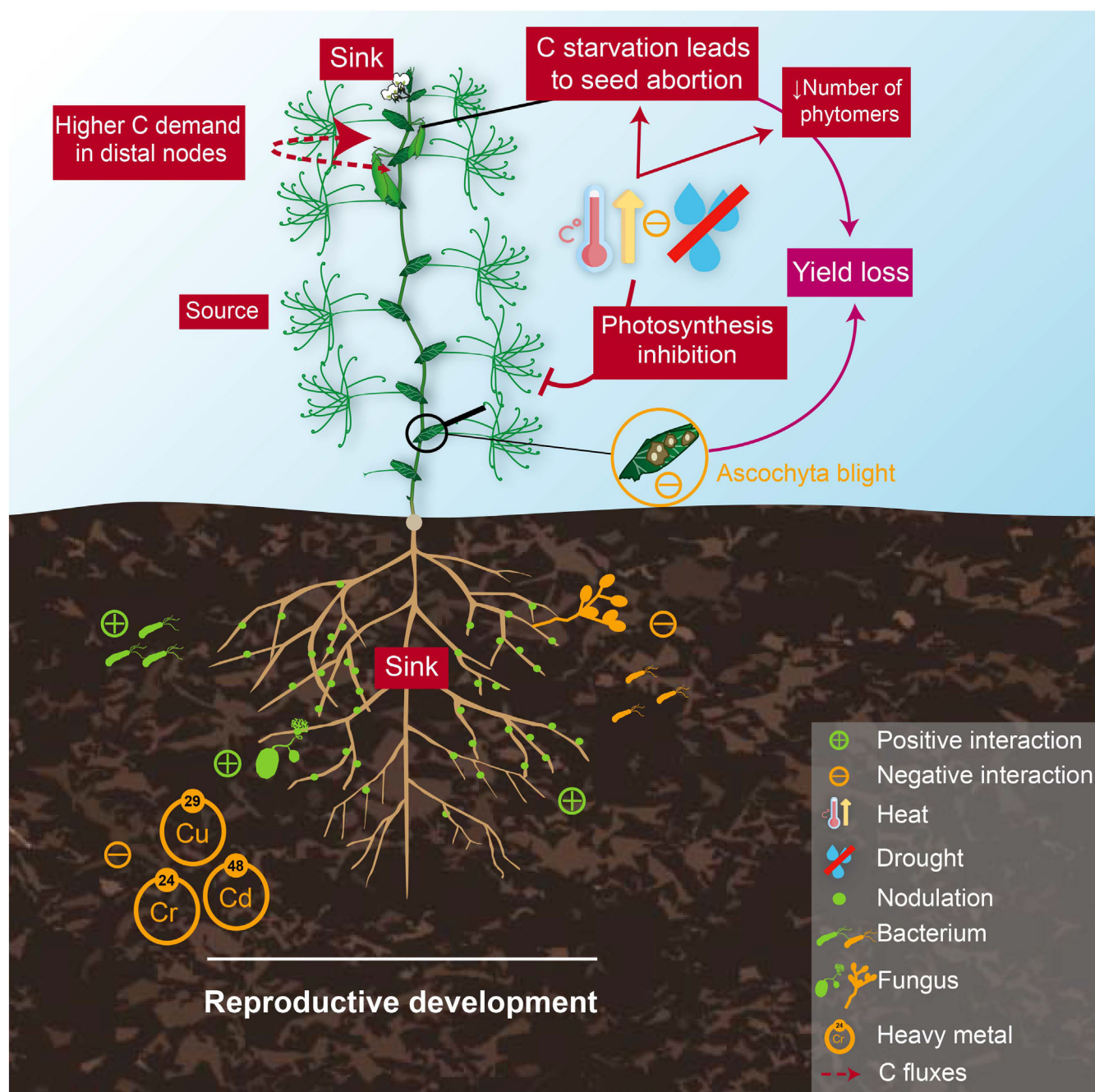


FIGURE 2 Schematic representation of carbon fluxes during reproductive development influenced by beneficial (green) or detrimental (yellow) environmental factors. Reproductive development is characterized by the formation of new sinks, changing trophic relations at the whole plant level. At this stage, newly developed seeds (distal nodes) tend to abort more than older ones (proximal nodes) due to their higher carbon demand, especially when environmental stresses such as drought, heat, heavy metals, or pathogens are involved. Drought and heat stress often occur at this stage due to seasonal climate, which can dramatically affect seed number and the number of reproductive phytomers. Moreover, the fungal pathogen causing *Ascochyta* blight can often infect the plant during its reproductive development leading to severe yield losses. Symbiotic microorganisms mostly play their part during vegetative development, but their beneficial effect enables better seed yield and quality at harvest

Bolero, *PsSWEET12* was highly expressed in mature and senescent leaves (Figure 3). In Bohatyr, clade III *SWEET* genes were expressed in sink and mature leaves but at a very low level in senescent leaves. In both cultivars, high expression of *PsCWINV* genes was measured in sink leaves as expected for organs with a high mitotic activity.

3.3 | Carbon fluxes in shoots in response to environmental constraints

Drought is the most important constraint limiting legumes growth and subsequent yield (Figure 1B). Water deficit leads to deep modifications of the plant primary and secondary metabolisms (Kumar

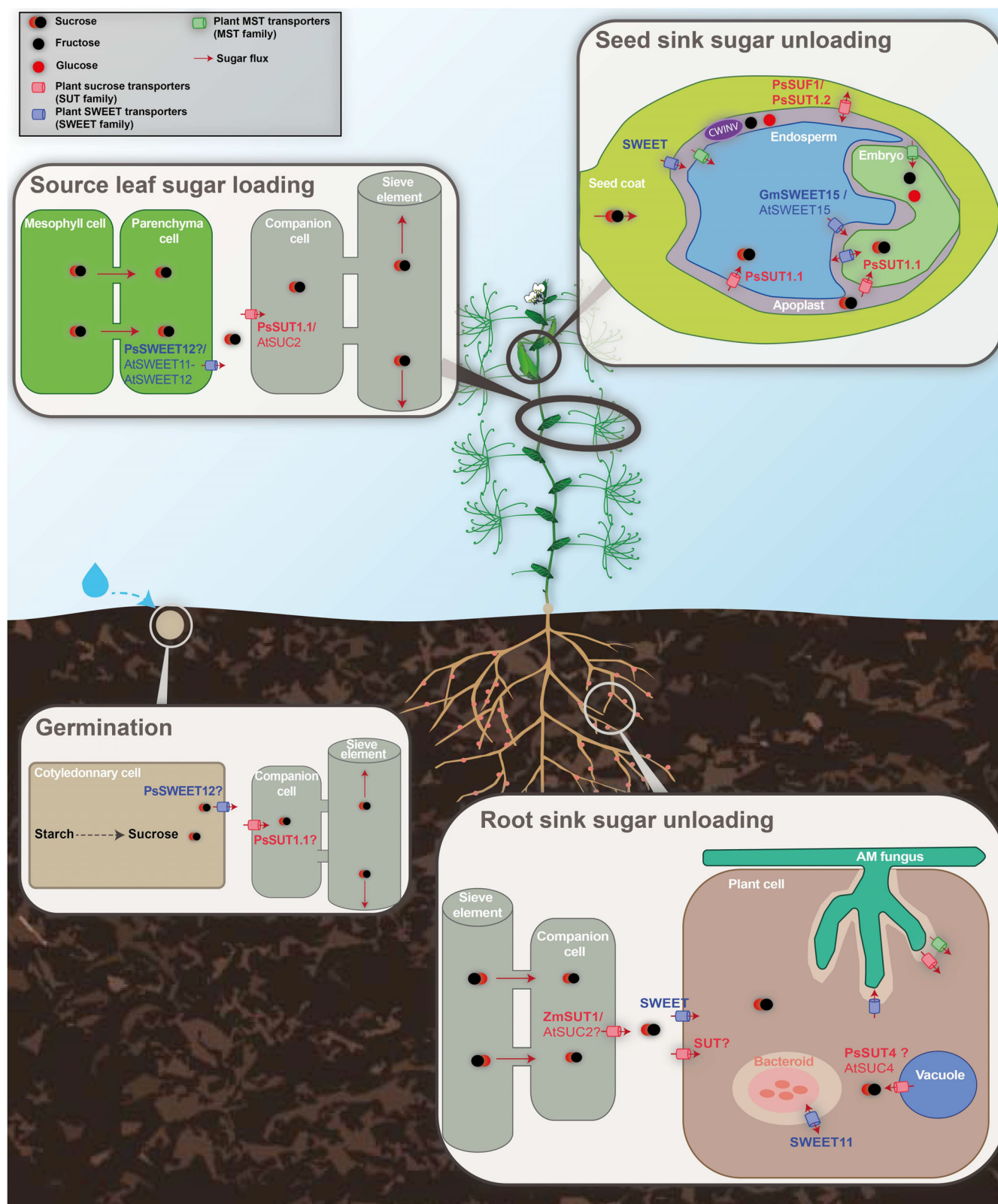


FIGURE 3 Legend on next page.

et al., 2021; Lahuta et al., 2022) (Table 1), as it decreases net photosynthesis and nutrient uptake. Hence, when facing drought, a major issue for the plant is to produce enough carbohydrates by

photosynthesis to sustain sink growth (Kumar et al., 2021; Nadeem et al., 2019). A study on the tolerance to water deficit of 49 pea cultivars indicated that soluble sugars could take part in leaf osmotic

adjustment and turgor maintenance to a bigger extent than proline (Sánchez et al., 1998). This study highlighted that sugars have a major role in osmotic adjustment since a positive correlation among the cultivars studied was found between the accumulation of soluble carbohydrates, especially myo-inositol and raffinose, their osmotic capacity and level of tolerance to stress (Lahuta et al., 2022; Sánchez et al., 1998; Sánchez et al., 2004) (Table 1).

In soybean, a study applying drought stress during the vegetative stage led to differential expression of genes involved in sugar metabolism and transport (Chen et al., 2016). Among them, glycolytic enzymes (hexokinase and fructokinase), as well as SWEET genes, were induced by drought. However, this induction of glycolytic enzymes was not observed in chickpea (Khanna et al., 2014), which suggests variability of response among legumes. In *Arabidopsis*, an enhanced export of sugar, linked to higher expression of *AtSUC2*, *AtSWEET11*, and 12—three genes associated with phloem loading (Figure 3)—was observed in response to water deficit (Durand et al., 2016). The same kind of investigations are still lacking in pea, and more studies on this topic are needed to uncover the mechanisms involved in sugar homeostasis and transport in response to drought. Nevertheless, some studies indicate that *afila* cultivars, with reduced leaf surface area, are less sensitive to drought than *leafy* cultivars thanks to a better ability to remobilize carbon to sinks (Baigorri et al., 1999; Couchoud et al., 2020). For instance, it was shown that in response to water stress, the semi-leafless cultivar (Solara) displayed an arrest in vegetative growth and an induction of leaf senescence, and its pod and seed dry weights did not decrease in comparison to the control condition (Baigorri et al., 1999). Furthermore, in pea senescing leaves, which are exporting carbohydrates, an increased expression of several clade II and III SWEETs as well as *PsSUT1* and *PsSUT2* genes (renamed *PsSUT1.1* and *PsSUT1.4*) was observed (Ninan et al., 2019).

Drought stress, and other abiotic stresses, such as high temperature and salinity (Figure 1B), lead to cellular dehydration in plants (Rane et al., 2021). To counteract this effect, plants synthesize osmolytes, such as sugars, which play different roles in carbon allocation, energy storage, signaling, or maintaining membrane integrity (Kumar et al., 2021; Rane et al., 2021) (Table 1). Moreover, to face

abiotic stress, plants produce reactive oxygen species (ROS), which induce oxidative stress and increase the accumulation of sugars, such as trehalose and sucrose to protect plant cells (Figuerola & Lunn, 2016; Kumar et al., 2021; Lin et al., 2019). A study on trehalose-6-phosphate phosphatase (TPP) overexpressing lines, the last enzyme implied in trehalose synthesis pathway, indicated that trehalose-6-phosphate (Tre6P) plays an important role in tolerance to several abiotic stresses, such as anaerobic conditions, salt, chilling, and cold stress (Figure 1B), in different plant species (Figuerola & Lunn, 2016). More precisely, Tre6P, a phosphorylated intermediate of trehalose biosynthesis, present in low concentration, seems to induce changes in sucrose concentrations, thus, promoting drought stress resistance (Figuerola & Lunn, 2016; Lin et al., 2019).

Even though cold stress can have severe effects on plant growth and subsequent yields at maturity (Figure 1B), pea, like most plants, has developed mechanisms of cold acclimation (Baldwin et al., 2014). Cold acclimation responses to chilling (0°C–15°C) and freezing temperatures (<0°C) have notably been studied by comparing behaviors of winter versus spring varieties. First, their response depends on light intensity. Under regular lighting, winter peas presented a higher freezing tolerance than spring peas (Bourion et al., 2003). Moreover, a close relationship was observed between the soluble sugar concentration in leaves before frost and the freezing tolerance of the genotypes. During cold treatment, the winter varieties were able to maintain their growth through an increase in soluble sugar levels in leaves and temporary starch storage (Bourion et al., 2003) (Table 1). However, such acclimation response was not observed in spring peas. Leaf architecture also seems to play a role in cold tolerance, specifically in new leaves developing during the cold period, according to a study comparing the photosynthetic activity of a *leafy* winter pea, two *afila* spring pea and an *afila* winter pea cultivar subjected to cold stress. The *leafy* winter pea (the most resistant cultivar) displayed the most rapid decrease in photosynthesis activity, which may be linked to its survival strategy (Husičková et al., 2019).

Waterlogging (or submergence) is detrimental to growth and yield and induces ROS accumulation because of oxygen deprivation stress (Pampana et al., 2016a, 2016b; Rane et al., 2021) (Figure 1B and

FIGURE 3 Schematic representation of sugar fluxes from source to sink organs mediated by sugar transporters during pea development. During germination, cotyledons are the main source organ and reserve degradation enables sucrose allocation towards sink radicle and shoots. When the first leaves are formed, photosynthesis is initiated and sucrose is released in the apoplast by SWEETs and retrieved in the companion cell, most likely by *PsSUT1.1*. Phloem loading is necessary to sustain the growth of sink organs. During the vegetative stage, roots are the main sinks. Sucrose is unloaded in roots by SUT and retrieved in root cells by SWEETs. Noteworthy, legumes can develop tripartite symbiosis. In AM symbiosis, sugars are exported by SWEETs towards the symbiotic interface across the periarbuscular membrane. Sucrose and monosaccharides can be retrieved back into the plant cell by MST (STP in *Medicago truncatula*) or SUT. Sugar transporters are also likely to be involved in plant-*Rhizobia* symbiosis, mainly by SWEETs (e.g., *MtSWEET11* in *M. truncatula*). Vacuolar transporters, such as SUT4-type, are also induced, especially in AM roots (Hennion et al., 2019), suggesting that remobilization of intracellular reserves occurs in colonized roots. During reproductive development, new sinks (flowers and seeds) are formed. Sugar unloading in the seed coat involves a symplastic pathway. Sucrose is released in the apoplast by SWEETs and SUT transporters. During embryogenesis, CWINV hydrolyses sucrose in glucose and fructose, which might be either loaded in the embryo and the endosperm either by MSTs or SWEETs hexose transporters. The expression of *PsSUT1.1* in the endosperm suggests that sucrose can be directly loaded in this tissue and escapes invertase hydrolysis. Sucrose can be exported from the endosperm by SWEETs (*GmSWEET15* in soybean). Cotyledonary cell expansion results in the progressive disappearance of the endosperm, which characterizes the transition from embryogenesis to seed-filling. During early seed-filling, invertase expression and activity decrease, and sucrose is directly imported to the cotyledons by *PsSUT1.1*, as starch and protein storage begin

Table 1). In relation to climatic fluctuations observed these last years, waterlogging is becoming a critical problem. By restricting oxygen diffusion in submerged tissues, aerobic respiration is impaired, and a shift occurs to anaerobic ethanolic fermentation (Phukan et al., 2018; Rane et al., 2021). Waterlogging impacts plant development by reducing photosynthesis, plant growth, nodule activity, and grain yield. Waterlogging damages increase as plants become older and advance towards the reproductive stage (Pampana et al., 2016a, 2016b; Rane et al., 2021). Photosynthesis is decreased by stomatal closure and the weak ATP production by anaerobic fermentation slows down plant growth. Sugar availability, metabolism, and transport are important components of the response to waterlogging, as for many other abiotic stresses (Phukan et al., 2018; Rane et al., 2021). In rice and pigeon pea, tolerant varieties accumulate a larger amount of soluble sugars than susceptible ones (Phukan et al., 2018). During waterlogging, *Arabidopsis* transgenic lines over-expressing a waterlogging-responsive ethylene response factor (*MaRAP2-4*) regulating *AtSWEET10* showed a higher stress tolerance in comparison to the wild type (Phukan et al., 2018). Indeed, to face waterlogging, plants could accumulate sugars, but this strategy might not be sufficient to survive under prolonged waterlogging stress. Plants may also use sugar resources to get their leaves out of the water through the rapid growth of the shoot system. These strategies are under the tight control of the source/sink relationship regulating carbon allocation (Phukan et al., 2018; Rane et al., 2021).

Waterlogging also induces anoxia in the soil, which can lead to an increase in toxic compound concentrations (Rane et al., 2021). The impact of cadmium on plant growth is mainly due to a lower chlorophyll content leading to a reduction of photosynthetic rate and an accumulation of oxygen free radicals, leading to possible leaf senescence (Sandalio et al., 2001) (Table 1). Soluble sugars could play a role in Cd stress response since a study on sensitive maize demonstrated that the more plants produced soluble sugars the higher the Cd concentrations were, indicating that this variety uses more carbohydrates to defend itself against Cd rather than to sustain its growth (Li et al., 2020).

Legumes are also affected by different fungal, bacterial, and viral diseases, as well as insect and nematode infections (Van Emden et al., 1988). The major pathogen infecting pea during early vegetative development is the Oomycete *Aphanomyces euteiches*, the causing agent of root rot disease (Figure 1B). Numerous pathogens, such as *Pythium* sp., *Phytophthora* sp., *Rhizoctonia solani*, or *Botrytis cinerea* are also responsible for “damping-off,” killing or weakening pea seedlings before or after their germination. Notably, these heterotrophic pests infect plants and feed on sugars. As such, pathogens have evolved an arsenal of sugar-splitting enzymes and sugar transporters to gain access to plant photosynthates (Doidy et al., 2012). For instance, the biotrophic rust fungus *Uromyces fabae* possesses a hexose transporter, *UfHXT1*, specially targeted to the plant-fungal interface (haustoria), thereby feeding on *Vicia faba* hexose (Voegelé et al., 2001). The activity of invertase enzymes in *P. sativum* also increased in response to *Erysiphe pisi* infection (powdery mildew), and the leaf starch content was also impacted (Storr & Hall, 1992) (Table 1). In response, plant

transporters are regulated to retrieve photosynthates back to the plant cell. For instance, the monosaccharide transporter *STP13* has long been shown to be regulated by multiple stresses, both biotic and abiotic. Notably, its expression is induced by several pathogens and contributes to plant resistance in different species (Yamada et al., 2016). In legumes, *MtSTP13.1* is involved in sugar competition when infected with the pea powdery mildew *Erysiphe pisi* and over-expression of *MtSTP13.1* promoted pathogen resistance in pea (Gupta et al., 2021a) (Table 1). Finally, SWEET transporters also play a key role in plant disease resistance. More precisely, a growing number of studies have shown that pathogens are able to modulate the expression of these sugar exporters to redirect sugar fluxes towards them (Gupta et al., 2021b; Lemoine et al., 2013). SWEET transporters represent a promising target for the development of resistant crop cultivars (Gupta et al., 2021b, see Section 6) and we identified 22 PsSWEET in *P. sativum* (Doidy et al., 2019). In conclusion, sugar transporters play crucial roles in plant-microbe interactions and legume species offer an excellent model to study them (Chandran, 2015; also see Section 3.3).

4 | CARBON FLUXES IN ROOTS DURING VEGETATIVE DEVELOPMENT

4.1 | Sugar unloading in root

Roots pattern establishment is divided into three steps. First, an initial lag phase during germination, followed by an early rapid growth during shoot development and a linear phase after flowering (Mitchell & Russell, 1971; Thorup-Kristensen, 1998; Vocanson et al., 2006). Root legume development starts with the rapid taproot elongation followed by lateral root emergence (Mitchell & Russell, 1971; Tricot et al., 1997). A decrease in root elongation rate was observed when C allocation starts from source leaves to roots, probably in link with the exhaustion of seed reserves (Tricot et al., 1997). The transition from heterotrophy to autotrophy seems to affect firstly lateral root development and later the taproot. Indeed, C supply sustains the growth of lateral root primordia, and depletion in C allocation reduces lateral root elongation and root branching before the taproot growth rate is affected (Tricot et al., 1997). This result indicates that the taproot displays a higher priority for C allocation compared to lateral roots (Tricot et al., 1997) (Figure 1B).

During the vegetative stage, roots and young leaves are major sinks (Wardlaw, 1990) and the hierarchy between sinks is determined by the strength of the sink (Ho, 1988). Sink strength corresponds to the ability to reduce photoassimilates in cells of the sieve tube at the sink level, thereby creating a hydrostatic pressure gradient favorable to long-distance transport of sucrose and unloading towards this sink (Wardlaw, 1990). The first step of sucrose unloading in sink organs involves a symplastic pathway (Patrick, 1997) (Figure 3), as observed in *Arabidopsis* root tips (Oparka et al., 1994). Beyond the phloem unloading zone, the type of transport varies according to the type of sink and the stage of development, but transport of sugars via the apoplastic pathway is possible and involves active SUT transporters

and SWEET facilitators (Chen, 2014; Durand et al., 2018; Lalonde et al., 2004) (Figure 3). Moreover, sugar transporters' expression is modulated by adverse conditions, highlighting that source-sink regulation for sucrose is affected by environmental factors (Durand et al., 2016; Lemoine et al., 2013).

Although carbon allocation to the roots is important during vegetative development (Voisin, 2003), some authors suggested that root growth stops during reproductive development due to reduced sink strength (Jeuffroy & Warembourg, 1991). Other studies showed that during seed-filling, a slow rate of root growth also takes place, which is associated with a decrease in lateral root emergence and root biomass (Armstrong et al., 1994; Salter & Drew, 1965).

4.2 | Carbon fluxes in challenging soil conditions

Root growth and development are strongly influenced by environmental factors, such as soil structure and climatic conditions (Ali-Khan & Snoad, 1977) (Figure 1B). When occurring at the start of the vegetative stage, drought negatively impacts seed germination and seedling growth with a reduction of shoot and root dry weights in different species, including in pea (Fahad et al., 2017). To face such water stress, the first plant responses include a decrease in photosynthesis and transpiration activities followed by an accumulation of osmoprotectants (non-reducing sugars, polyols, amino acids, etc.) in both roots and leaves (Kumar et al., 2021; Lahuta et al., 2022). This higher osmotic potential maintains root water uptake from the soil (Kumar et al., 2021; Lahuta et al., 2022) (Table 1). In seven-day-old pea seedlings, an earlier accumulation of sucrose was observed in roots than in epicotyl after 24 h of dehydration, followed by an accumulation of galactinol and raffinose (RFOs family) in both organs (Lahuta et al., 2014). Therefore, drought stress increases the content of sucrose, glucose, and sugar alcohol in the phloem sap of pea to sustain osmotic potential, water content and transport, and maintain cell metabolism (Blicharz et al., 2021) (Table 1). Thus, water deficit response induces metabolic modifications, some of which are linked to source/sink relationships (Lemoine et al., 2013). In *Arabidopsis*, a preferential C allocation towards roots was observed during water deficit to sustain root growth. This phenomenon was associated with an induction of *AtSWEET11*, *AtSWEET12*, and *AtSUC2* genes, which are responsible for phloem loading in leaves and might also be involved in phloem unloading in roots (Durand et al., 2016) (Figure 3).

In field conditions, a drought episode may be followed by strong rainfall leading to flooding. Autumnal grain legumes present a higher risk of being exposed to such submersion (Pampana et al., 2016a). During waterlogging, inhibition of aerobic respiration and TCA dysfunction are observed in submerged tissues associated with ROS increase, leading to a decrease in shoot and root growth (Table 1) (Pampana et al., 2016b; Rane et al., 2021). Limiting oxygen availability observed during waterlogging enhances alcoholic fermentation, an adaptive mechanism to provide energy to the plants facing this stress. Moreover, waterlogging induces root architecture arrangement with the formation of aerenchyma in the cortex for storing O₂, stem

hypertrophy, and formation of adventitious roots. This stress also impacts photosynthesis activity, plant development, seed productivity, and nodule integrity (Pampana et al., 2016a). Both synthesis of fermentable sugars and release of hydrolyzed sugars contribute to waterlogging tolerance in crop plants (Goyal et al., 2020).

4.3 | Carbon fluxes in beneficial microorganism interactions

Legumes are notably cultivated for their agroecological value through their beneficial associations with microorganisms. Symbiosis of legumes with *Rhizobia* leads to an improved nutritional status, mainly in nitrogen (Figure 1B), which in turn leads to increased photosynthetic rates and beneficial effects on plant growth and yield. Not only is pea crop able to establish symbioses with N-fixing bacteria, but it simultaneously interacts with arbuscular mycorrhizal fungi (AMF) supplying phosphate (Figure 1B). In agroecology, this symbiotic interaction is called "tripartite" because it implies three partners: the plant, the bacteria, and the fungi. Legumes exploit this synergistic biofertilization from both the bacteria and fungi, thereby improving yield and grain quality.

In return, legumes provide a significant amount of its fixed photosynthetic carbon to the symbiont (Kaschuk et al., 2009). Noteworthy, the increased photosynthetic rates not only result from the increased nutrient uptake provided by these symbionts, but also from sink stimulation (Kaschuk et al., 2009). To our knowledge, no study has estimated plant carbon fluxes in tripartite symbiosis, but authors rather focused on the improved seed quality and yield gained through synergistic symbioses (Geneva et al., 2011; Shinde & Thakur, 2016; Xavier & Germida, 2003). In both mycorrhizal and rhizobial interactions, sugar transport systems are also involved, and we previously speculated that a common transport pathway might be shared between both symbioses (Hennion et al., 2019). Indeed, the expression of several sugar transporters is regulated in mycorrhizal and *Rhizobia* interactions (Banasiak et al., 2021; Doidy et al., 2012), suggesting that they may participate in sucrose distribution towards the symbionts. Just to name a few, this concerns several SUTs and SWEETs in legumes: MtSUTs (Doidy et al., 2012), GmSUT1 (Deng et al., 2021); MtSWEET1b (An et al., 2019) (Figure 3), MtSWEET11 (Kryvoruchko et al., 2016), and LjSWEET3 (Sugiyama et al., 2017). Orthologous genes in pea also seem regulated in plant-microbe interactions (Alves-Carvalho et al., 2015; Doidy et al., 2019; Zhou et al., 2007). Very few studies have so far focused on the molecular players involved in the synergistic co-inoculation of bacterial and mycorrhizal fungi. Up to now, the only information comes from an elegant split-root system, showing that legumes allocated more carbon to *Rhizobia* under nitrogen demand, but more carbon to the fungal partner when nitrogen is available in the fungal compartment (Kafle, 2018). This report also highlighted several SWEETs (*MtSWEET1b*, *MtSWEET6*, *MtSWEET11*, *MtSWEET12*, *MtSWEET15c*, and *MtSWEET15d*) regulated in *Medicago truncatula* roots depending on the colonization with different root symbionts subjected to different nutrient supply conditions.

Plants, including legume species, also interact with a diverse set of non-pathogenic rhizobacteria species (Figure 1B), commonly named Plant Growth Promoting Rhizobacteria (PGPR). PGPR can confer to plants an improved growth and/or tolerance to various biotic and abiotic stresses and present a high potential for agricultural applications. Currently, this prospect is limited by the lack of information on the molecular mechanisms involved in these biological processes (Vacheron et al., 2013). Interactions of plants with these beneficial soil microorganisms involve the liberation of plant organic compounds via rhizodeposition, which is itself dependent on the plant carbon budget (Lepinay et al., 2012). As mentioned above, a growing body of evidence demonstrates the importance of sugar transport in plant-pathogen resistance and in plant-microorganism mutualistic symbioses. In contrast, the role and regulation of sugar transporter activities in plant-PGPR interactions remain largely unknown (Hennion et al., 2019). Using the model plant *Arabidopsis* and a collection of PGPR strains, it was recently shown that PGPR can induce major transcriptional changes in plant sugar transport (Desrut et al., 2020; Desrut et al., 2021). Moreover, it was shown that *AtSWEET11* and *AtSWEET12*, two sugar transporter genes whose expression is repressed by the well-characterized PGPR strain *Pseudomonas simiae* WCS417r, are functionally involved in its plant growth-promoting effects, possibly by controlling the allocation of carbon resources (Desrut et al., 2020).

In addition to their positive effects on plant productivity under optimal growth conditions, evidence in the literature shows that beneficial microorganisms, including *Rhizobia*, AMF, and PGPR, are also efficient in alleviating the harmful effects of drought and other abiotic stress in legumes (reviewed in Nadeem et al., 2019). Such research area should help improve our understanding of plant resilience to its environment. Although many studies have focused on sugar transporters' expression in N-fixing and AM symbioses, much more attention should be paid to their role in stress acclimation.

5 | CARBON FLUXES DURING FLOWERING

The transition from vegetative to reproductive development implies the emergence of new sink organs (flowers and fruits) (Figure 2) and occurs in response to environmental factors and internal stimuli (for a review see Weller & Ortega, 2015). Flowering time is influenced by photoperiod (Lejeune-Hénaut et al., 1999) and temperature (Alcalde et al., 2000; Murfet & Reid, 1973). In legumes, the relationship between sugars and induction of flowering remains to be uncovered, although resource availability is tightly linked to flower abortion (Guilioni et al., 1997). In eudicots, floral meristem initiation, floral bud development, and transition to mature flowers depend on C provided by photosynthesis (Patrick & Colyvas, 2014). Indeed, in several species, the concentration of sucrose in the phloem sap increases to supply shoot apical meristem with sucrose and induces floral transition (Cho et al., 2018; Yoon et al., 2021). In soybean, abortion occurs more frequently during anthesis, which corresponds to a decrease in photo-assimilates imported into floral structures (Patrick & Colyvas, 2014). A

study on the late-flowering phenotype of the FT mutant in *Arabidopsis* further demonstrates that sucrose functions downstream of *CONSTANS* (CO) and upstream of *FLOWERING LOCUS T* (FT) (Cho et al., 2018; Yoon et al., 2021). Moreover, in *Arabidopsis*, Tre6P, which is synthesized in the phloem companion-cell-sieve element complex, acts as a signal for sucrose availability. Indeed, Tre6P favors sucrose demand of growing sink organs and its involvement in the flowering process has been recently identified (for review see Fichtner & Lunn, 2021).

Sucrose demand by sink organs is controlled by SUT and SWEET transporter families (Chen et al., 2010; Schneider et al., 2012; Sivitz et al., 2007). Several of them are specific to the reproductive organs and their high level of expression during flowering and fertilization indicates the importance of sugar exchanges in these processes (Andrés et al., 2020; Durand et al., 2018; Gu et al., 2020; Iftikhar et al., 2020). In pea, multiple sugar transporter and invertase genes were specifically induced in flowers (Doidy et al., 2019; Morin et al., 2022), but their expression pattern has been much more detailed in other model species. For instance, a study in petunia (*Petunia axillaris*) at five flowering stages indicates an increased expression of two SUC genes (*PaSUT1* and *PaSUT3*) and five SWEET genes (*PaSWEETS13c*, *PaSWEET9a*, *PaSWEET1d*, *PaSWEET5a*, and *PaSWEETS14a*) during floral development. Other SUT and SWEET genes are expressed during specific stages of flowering development (Iftikhar et al., 2020). As in *Arabidopsis* (*AtSWEET9*, Lin et al., 2014), *PaSWEET9c* is specifically expressed in nectaries of petunia (Iftikhar et al., 2020). Moreover, *PaSWEET10a* and *PaSWEET10b* display a higher expression in the early flowering stage in petunia (Iftikhar et al., 2020) like *AtSWEET10*, their ortholog in *Arabidopsis*, whose expression has been found induced by *FLOWERING LOCUS T* (FT) (Andrés et al., 2020).

Drought stress mostly occurs during flowering time in pea (Figure 2). Indeed, since winter and spring varieties flower, respectively, at the beginning of April and early June, pea often faces drought events during its reproductive development. Legumes are highly vulnerable to drought during the flowering phase, which leads to a shorter flowering period, fewer flower, and pod numbers, and a significant reduction in seed yield (Nadeem et al., 2019) (Table 1). Water stress applied at the flower onset also led to a marked decrease in biomass of non-reproductive organs in pea (Prudent et al., 2016) (Table 1). In pigeon pea (*Cajanus cajan*), water deficit applied during flowering caused over 50% reduction in seed yield, probably due to reduced photosynthesis activity leading to a disturbance of assimilate partitioning (Fahad et al., 2017). Floral organs are very strong sinks, especially during anther development when sugar import is ensured by cell wall invertases (CWINV), sucrose synthases (SUS), and sugar transporters (STP) (Sinha et al., 2021; Yu et al., 2019). Water deficit notably reduces invertase activity, preventing pollen from metabolizing sucrose to hexose, and thus, leading to sterility (Yu et al., 2019).

As high temperatures are often associated with water deficit, photosynthesis activity, and grain yield are negatively impacted by these stresses (Guilioni et al., 1997; Rane et al., 2021) (Table 1). Both drought and heat stress impact source/sink relationship by decreasing

photosynthesis rate and sucrose export to sink organs (Fahad et al., 2017; Hageman & Van Volkenburgh, 2021). This induces impairment in sugar availability (import and utilization) during reproductive growth by reducing the enzyme activity involved in sugar metabolism and transport (Li et al., 2015; Sinha et al., 2021; Yu et al., 2019). Interestingly, drought or heat stress-tolerant genotypes are able to maintain sugar concentration and partitioning (Dong & Beckles, 2019; Li et al., 2015; Sinha et al., 2021).

6 | CARBON FLUXES DURING REPRODUCTIVE DEVELOPMENT

6.1 | Filling carbon nutrients and sugar signals during seed development

Once flowers are pollinated, seed development occurs in a series of temporally and spatially defined steps. In *Fabaceae*, seed development can be divided into three phases: embryogenesis, a phase of cell division, followed by seed-filling, a phase of cell expansion, and finally a phase of desiccation/maturation (Ruan et al., 2012; Wang et al., 2019; Weber et al., 2005). Seed development highly depends on nutrient remobilization through source-sink long-distance transport driven by seed sink strength (Hageman & Van Volkenburgh, 2021; Lu et al., 2020; Pampana et al., 2016a, 2016b; Weber et al., 1997b). This latter is promoted by embryonic cell division, which occurs quicker in seeds from distal nodes, where mitotic activity is higher than in proximal ones (Munier-Jolain & Ney, 1998; Munier-Jolain & Salon, 2003). This is potentially linked to the higher sink strength of distal nodes (Munier-Jolain & Salon, 2003). As seed abortion is directly linked to C availability, seeds from distal nodes tend to abort more due to their higher demand (Guilioni et al., 2003; Ney et al., 1993), as shown by the decrease of seed number in these nodes (Jeuffroy & Devienne, 1995) (Figure 2).

Seed development is highly dependent on carbon remobilization and allocation mediated by sugar transporters. One day after fertilization in pea, an increase in the expression of *PsSUT2* (renamed *PsSUT1.4*) and *PsSUT5* (renamed *PsSUT1.2*) was observed in flowers, suggesting that these transporters may potentially be involved in sucrose transport to sustain mitotic activity and maintain osmotic pressure for embryonic growth (Smitha Ninan et al., 2017). First, in pea (Tegeder et al., 1999) and in faba bean (*Vicia faba*) (Offler et al., 1989), nutrients are unloaded into the seed coat from the chalazal vein through a symplastic pathway (Patrick, 1997; Van Dongen et al., 2003) (Figure 3). Then, in developing seeds, maternal tissues are physically separated from filial tissues, which implies the contribution of sugars transport systems (Lu et al., 2020; Tegeder et al., 1999; Weber et al., 1997a; Zhou et al., 2007). Here, export of sugars from the seed coat to the apoplast may involve both a passive (de Jong et al., 1997; Zhou et al., 2007) and an active component (Figure 3). At the molecular level, sugar provision towards the embryo is highly regulated by sugar transporters and invertases (Doidy et al., 2019; Morin et al., 2022) (Figure 3). During the early embryonic development, a

cell-wall bound invertase activity has been observed in the seed coat of legumes. In pea and in faba bean, this activity is associated with a high level of glucose and fructose in the apoplast surrounding the embryo (Weber et al., 1996) (Figure 3). Thus, invertase controls the ratio of sucrose to hexose and is likely a signal for the high mitotic divisions required during embryogenesis (Morin et al., 2022; Weber et al., 1995). During the later stages of embryogenesis, it is commonly accepted that sucrose is released from the seed coat. In pea, several studies have shown that sucrose facilitators *PsSUF1* (renamed *PsSUT1.2*) and *PsSUF4* (renamed *PsSUT4.2*) are expressed in transfer cells of the seed coat parenchyma to allow sucrose unloading to the seed apoplast (Zhang et al., 2007; Zhou et al., 2007) (Figure 3).

After its translocation in the apoplast, the outcome of sucrose depends on the phase of seed development. During the endosperm cellularisation (heart and torpedo stages), it has been shown in faba bean (Weber et al., 1996) that acid invertases cleave sucrose into hexoses (Figure 3), creating a favorable sucrose gradient between the seed coat and the apoplast, and thus drive sucrose unloading (Weber et al., 1995). Expression of *PsSUT1.1* during this step also suggests that part of sucrose escapes invertase hydrolysis and is directly imported into transient endosperm and embryo cells (Melkus et al., 2009; Rosche et al., 2002) (Figure 3). During the cotyledon development stage, which starts at the torpedo stage, sucrose is taken up from the apoplast into the cotyledons thanks to *PsSUT1.1*, a proton-coupled sucrose transporter localized in the cotyledon epidermal cells (Tegeder et al., 1999; Weber et al., 1997a; Zhou et al., 2007) (Figure 3). Interestingly, *PsSUT1.1* overexpression resulted in increased sucrose content in developing seeds, and plants eventually produced more protein and starch, as well as higher seed yield (Lu et al., 2020; Zhou et al., 2007).

In soybean and faba bean, *GmSWEET15a/b* mediates sucrose transport from the endosperm to the embryo (Figure 3), while the high hexose status driving the embryonic growth through cell division is maintained by *VfCWINV1* (Wang et al., 2019; Weber et al., 1996). In *Arabidopsis*, *SWEET* genes of the clade III, *AtSWEET11* and *AtSWEET15*, are also implicated in this sucrose transfer from the endosperm to the embryo (Chen et al., 2015). In pea, we identified the gene orthologs, *PsSWEET15* (Doidy et al., 2019) and *PsCWIN1.2* (Morin et al., 2022), as highly expressed during the embryonic stage and regulated by water stress (Figure 3). When embryogenesis ends, the Final Stage in Seed Abortion (FSSA) is passed, thus the seed can no longer abort (Duthion & Pigeaire, 1991). Altogether this emphasizes the important role of *SWEET* and *INV* during early seed development, thus controlling abortion rates and final seed size (Morin et al., 2022; Wang et al., 2019; Weber et al., 1996).

During the seed-filling stage, growth continues through cell expansion, and simultaneously sucrose assimilation increases, and soluble protein and starch synthesis begin (Patrick & Offler, 2001). A decrease in hexose to sucrose ratio is marked by a sharp decrease in *PsINV* gene expression and enzymatic activities (Morin et al., 2022; Weber et al., 2005). Notably, this temporal downregulation of *PsINV* activity results from the progressive mechanical crushing of seed coat cells expressing the enzyme (Weber et al., 1995). Sucrose is released

from the seed coat and taken up directly by the cotyledons through PsSUT1.1 and stored as starch (Hageman & Van Volkenburgh, 2021) (Figure 3). In pea, sucrose fluxes from the seed coat to the embryo are coordinated through turgor homeostasis, detecting variation of the apoplastic sucrose pool through turgor modifications, and regulating PsSUT1.1 expression (Zhou et al., 2009). This enables a balanced control between sucrose supply and demand of the embryo. While invertase activity declines, sucrose synthase and sucrose synthase phosphatase are strongly expressed in the cotyledons, thereby promoting the onset of starch synthesis and accumulation (Lu et al., 2020; Weber et al., 1997a; Yang et al., 2019; Yu et al., 2020).

In pea, starch synthesis during seed-filling is promoted by Tre6P and there is evidence that the plant hormone auxin plays an important role in controlling sucrose utilization (McAdam et al., 2017). Indeed, it has been observed that Tre6P stimulates auxin synthesis through the induction of TRYPTOPHANE AMINOTRANSFERASE RELATED2 (TAR2). This study concludes that a certain auxin level is needed for the action of Tre6P for promoting seed-filling and auxin might act downstream of Tre6P to accelerate storage processes (Meitzel et al., 2021). The last stage of seed development, dormancy, is dependent on FLOWERING LOCUS T in pea, and FT is also regulated by Tre6P signaling pathway in *Arabidopsis* silique (Fichtner & Lunn, 2021; Meitzel et al., 2021). Moreover, in *Arabidopsis*, ABA is implicated in seed dormancy driven through the ABA INSENSITIVE4 gene expression associated with AtTPS1 (TREHALOSE-6-PHOSPHATE SYNTHASE 1) gene expression. These results indicate that Tre6P might have a role in seed maturation since trehalose pathway mutants had lost the ABA sensitivity and could not enter the dormancy stage (for review see Fichtner & Lunn, 2021).

6.2 | Carbon fluxes towards seeds are impacted by environmental changes

As discussed above, drought negatively impacts seed yield (Sánchez et al., 1998; Sousa-Majer et al., 2004; Strydhorst et al., 2015) (Figure 2) because of an increase in flower and pod abortions reducing seed number (Guilioni et al., 1997) (Table 1). Water deficit also directly impacts seed development, and this more strongly during early seed development (prior FSSA) than at later stage of seed-filling (Mahieu et al., 2009). When drought stress occurs during the filling stage, individual seed weight and phytomer number decrease (Guilioni et al., 2003; Nadeem et al., 2019; Ney et al., 1993) (Table 1) while leaf senescence is accelerated (Rane et al., 2021), therefore affecting source-sink relationships (Chen et al., 2006). Drought (and heat stress) changes the distribution of pea seeds along the stem (Guilioni et al., 2003). Indeed, pods located on basal phytomers had more seeds in response to stress conditions than upper nodes. This trend is likely linked to the higher demand of upper nodes (Munier-Jolain & Salon, 2003) (Figure 2), which may not be fulfilled because of a decrease in net photosynthesis during stress conditions (Guilioni et al., 2003).

Interestingly in common bean, sucrose content in seeds increased more in the drought-tolerant variety than in the sensitive one when

water deficit was applied during early seed-filling (Gebeyehu et al., 2011). However, both varieties displayed lower starch accumulation in seeds, potentially due to limitations in assimilate availability by the source. However, in soybean, drought applied during reproductive development increased soluble sugars in leaves and reduced photosynthetic rates (Du et al., 2020). This increase of sugars in leaves may increase the amount of sucrose loaded into the phloem for the nutrition of sink organs. In parallel, activities of sucrose phosphate synthase, sucrose synthase and acid invertases, as well as the expression of their respective encoding genes, increased in leaves (Du et al., 2020). The authors also showed higher expression of genes related to sugar metabolism and transport in developing seeds, suggesting maintenance of the push and pull mechanism during drought stress. Indeed, in common bean, tolerance to water deficit may be linked to both sink strength maintenance and the capacity of the source organs to produce and export carbohydrates towards sink organs (Hageman & Van Volkenburgh, 2021). However, Hageman & Van Volkenburgh (2021) describe that source strength is not a good indicator for yield (unlike the pod harvest index), both under normal growing conditions and during water stress.

During drought stress, stomatal closure in leaves leads to a reduction in photosynthesis in green peas, which limits C availability and causes yield losses (Nemeskéri et al., 2015). In addition to its effect on stomatal closure during water deficit, ABA also acts on the loading of resources (Hageman & Van Volkenburgh, 2021). For instance, ABA is known to increase the expression of cell wall invertase inhibitor genes resulting in decreased activity of CWINs involved in maintaining sucrose gradient and sink strength, which at term impact seed size (Ruan, 2014; Ruan et al., 2010; Westgate et al., 1996).

Pathogens also influence the proper course of reproductive development and source-sink relationships. For instance, *Ascochyta* blight (Figure 2) is caused by a fungus (*Didymella pinodes*) that penetrates through stomatal apertures in the spring and its severity increases after flowering, causing severe yield loss, especially in early-maturing varieties (Bretag et al., 1995) (Table 1). Up to now, breeding for resistant cultivars with suitable agronomic traits has had limited success (Khan et al., 2013). The C/N ratio in seeds is also affected by an increased protein concentration and a decreased starch content in response to *Ascochyta* blight pathogen (Garry et al., 1996) (Table 1). Results from a comprehensive study comparing the metabolic and proteomic profiles of the susceptible pea cultivar Messire with the more tolerant cultivar Protecta revealed that enhanced tolerance towards *D. pinodes* is notably associated with higher sugar levels, including a significant increase in maltose and fructose as well as in the TCA cycle compounds, pyruvate and citrate (Turetschek et al., 2017). Altogether, these results suggest that, during the defense response against necrotrophs, plant resistance is enhanced if cell death is not triggered, which limits the release of sugars to the pathogen. Plant sugar levels then remain high because they cannot be metabolized by the fungi (Turetschek et al., 2017). In a study focusing on unraveling resistance genes to this pathogen in the *Cicer* genus, the authors identified a probable sugar transporter (Newman et al., 2021). This transporter may be involved in retrieving sugars

from the apoplast to limit extracellular sugar pools available for the pathogen. To our knowledge, very little data are available to date on pea sugar homeostasis and transporter in relation to these different environmental conditions. Thus, research strategies are currently being developed to unravel the mechanisms that should contribute to the creation or selection of new pea varieties more resilient to the present and future challenging environments.

Several studies have shown that beneficial microorganisms, previously described in this work, often result in improved yield and seed quality at maturity (Geneva et al., 2011; Shinde & Thakur, 2016; Xavier & Germida, 2003), and this occurs through their effect during the different stages of plant development (Figures 1 and 2) and in response to various abiotic stresses (Nadeem et al., 2019). Therefore, exploiting such associations with beneficial microbes represents a promising strategy to increase legume crop resilience towards environmental changes, especially during their crucial developmental phase of seed production.

7 | FUTURE MILESTONES: ENGINEERING SUGAR TRANSPORTERS TO IMPROVE SEED YIELD, QUALITY, AND STRESS RESILIENCE IN LEGUMES

We reviewed here the importance of C fluxes and resource allocation during key developmental processes of *P. sativum* and its multifactorial interactions with the environment. Selection of new pea genotypes for higher yield stability should now consider the genotype-environment interactions and their impact on shoot (source), root and seed (sink) developments (Vocanson et al., 2006).

A first breeding strategy should focus on the phenotypic diversity of pea. Indeed, pea plant architecture is an important factor in determining yield and recent works highlight possible targets to increase plant productivity and stress resistance (Guo et al., 2020). In pea, the impact of water deficit seems to be tightly linked to leaf architecture with a better resistance for *afila* than *leafy* varieties (Baigorri et al., 1999). In fact, the absence of leaflets in *afila* genotypes does not negatively impact photosynthates export towards pod (Harvey, 1974). The author hypothesized that a better illumination, and so a higher photosynthesis of the pods in the *afila* genotypes, could explain this lack of difference. Therefore, the *afila* genotypes (widely cultivated nowadays) seem comparable to classical *leafy* phenotypes, in terms of C assimilation and export to the pod (Baigorri et al., 1999). The root system architecture is also a key feature to take into account in the next breeding programs to improve stress resilience and nutrient remobilization, since yield stability in field conditions was correlated to the rooting depth (Bertholdsson, 1989). Moreover, genotypes displaying longer roots during early development showed increased root growth time and water use efficiency, leading to a deeper rooting at later developmental stages (Thorup-Kristensen, 1998). This observation could be linked to a better use of starch by the roots. As starch is the main form of C storage, starch metabolism could be a possible target to

explore adaptive changes in the source-sink allocation of plants to face abiotic stress (Dong & Beckles, 2019; Li et al., 2015).

Secondly, exploiting *Pisum* genetic variability should also enable breeders to create novel pea varieties more productive and stress-resilient. Future research strategy needs to focus on the regulation of assimilate partitioning and carbon metabolism in sink organs to improve grain filling under adverse conditions (Dong & Beckles, 2019; Fahad et al., 2017; Hageman & Van Volkenburgh, 2021; Li et al., 2015). Thus, characterization of the molecular actors involved in carbon partitioning between source and sink organs is key to achieving this goal. Multiple mutants in carbon utilization have been described with defects in the starch metabolic pathway in pea (Yu et al., 2020). For instance, molecular biologists have re-discovered in the 90s that the wrinkled trait (*rr*), initially observed by Gregor Mendel, was due to a disruption in *SBE1*, a gene responsible for branching starch molecules (Bhattacharyya et al., 1990). However, to the best of our knowledge, only a single mutant is available for sugar transporters in pea. Lines overexpressing *PsSUT1.1* showed increased sucrose phloem loading and nutrient fluxes towards sink organs (Figure 3) and produced higher seed yield with more protein and starch (Lu et al., 2020). Sugar transporters like *PsSUT1.1* (Lu et al., 2020) that play a central role in phloem loading in source organs and control sink carbon storage and seed yield (Figure 3), represent therefore key targets for breeders and farmers. The potential of harnessing carbon fluxes is just starting with the recent identification of sugar transport systems in legume genomes (Doidy et al., 2019).

In addition, uncovering the influence of environmental factors along the plant lifecycle is an important area of research. In pea, in response to drought stress, vegetative growth was stopped and leaf senescence was induced so that similar partitioning of dry weight to pod and seeds was maintained as in control conditions (Baigorri et al., 1999). During this last stage of development, an increased expression of several clade II and III SWEETs associated with a high level of *SUT1* and 2 was noticed in pea leaves (Ninan et al., 2019). Functional characterization of these genes might help improve our understanding of carbon flux regulation in response to water stress. Moreover, Hageman and Van Volkenburgh (2021) propose that genetic lines with decreased sensitivity to ABA, which could maintain a strong sink strength and a higher yield, might represent a promising way to identify tolerant genotypes to water deficit. This perspective should be taken with caution since a loss of ABA sensitivity could increase water sensitivity in some species. As this review points out, some knowledge is already gathered on such actors; however, the complete picture is not yet drawn, and future studies will enable us to implement a model describing carbon fluxes in *P. sativum* and create new varieties more resilient to environmental changes. This could be reached through agronomic practices, as well as conventional breeding approaches, promoting beneficial microorganisms, or quantitative trait loci (QTLs) analyses (Nadeem et al., 2019).

Other promising ways to improve pea genotypes are biotechnology and functional genomics. New gene-editing technologies, such as CRISPR/Cas9, represent promising tools for legume improvement (Bhowmik et al., 2021; Nadeem et al., 2019). For instance, CRISPR/

Cas9 has successfully been developed in chickpeas with associated drought tolerance (Badhan et al., 2021). Targeting sugar transport system, such as vacuolar components maintaining cell turgescence in response to water deficit (Slawinski et al., 2021), may also be a hopeful opportunity to develop climate-resilient crops. In conclusion, plant membrane transporters represent a key target to increase crop yield and quality, as well as to improve the sustainable production of nutritious foods (Banasiak et al., 2021; Schroeder et al., 2013).

AUTHOR CONTRIBUTIONS

All authors contributed to proofreading the manuscript. Amélie Morin contributed to the part on germination and reproductive development, designed Figures 1, 2 and 3, and Table 1. Laurence Maurousset contributed to the part on abiotic stresses during vegetative and reproductive stages. Cécile Vriet contributed to the part on biotic interactions during vegetative and reproductive development. Rémi Lemoine contributed to the part on leaf development. Joan Doidy contributed to the part on biotic interactions during vegetative and reproductive development, the introduction and the abstract. Nathalie Pourtau contributed to the part on root development, abiotic stresses during the vegetative stage and edited the manuscript.

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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ENDNOTE

¹ Doidy et al. (2019) and Morin et al. (2022) proposed a new nomenclature for *PsSUTs*, *PsSWEETs*, *PsMSTs*, and *PsINV*s based on a phylogenetic analysis of legume and *Arabidopsis* sequences, which we will refer to along this review.

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