Theor. Exp. Plant Physiol. (2025) 37:10
https://doi.org/10.1007/s40626-024-00352-1

Distinct metabolic profiles of key metabolites in sugarcane leaves and culms highlight their potential roles in growth and development

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Received: 20 May 2024 / Accepted: 6 September 2024

Abstract Carbohydrates, hormones, and other metabolites integrate a system linking the internal energy status and external stimuli that influences plant growth and survival. Here, we measured the concentrations of free amino acids, polyamines (PAs), and the phytohormones indole-3-acetic acid (IAA) and abscisic acid (ABA) in leaves and culms of sugarcane during the crop cycle (1 to 12 months) in the field. Leaves accumulated PAs in all months but this profile was not observed in the culm. Amino acid concentrations were more constant in the leaf than in the culm, and total amino acid concentration in this organ was 12-fold higher in the first month. The last month of sugarcane development was marked by increased concentrations of IAA and ABA in the leaves. These findings indicated that sugarcane has metabolic strategies to cope with developmental and environmental challenges, influencing the metabolic flow of each organ and impacting adaptive physiological responses. Together, these changes provide insights into distinct metabolic profiles of each organ throughout development and pave the way

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Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s40626-024-00352-1.

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Published online: 22 January 2025

for a more integrative understanding of the biological functioning of sugarcane in the field, which can contribute to future strategies to improve yield performance.

Keywords Sugarcane · Amino acids · Polyamines · Hormones

1 Introduction

Carbohydrates, amino acids, and hormones trigger adaptative responses to the environment and regulate many aspects of plant growth and development (Minocha et al. 2014; Ferreira et al. 2018; Emenecker and Strader 2020). Carbohydrates are produced by photosynthesis and their production, transport, consumption, and storage are connected to cellular metabolic activities, organ identity, and developmental phases (Smith and Stitt 2007). Therefore, the integrative plant perception and management of carbohydrate concentrations could serve as a control mechanism to integrate external environmental factors, nutrient homeostasis, developmental programs, stress response, and plant metabolism (Smith and Stitt 2007; Li and Sheen 2016).

Polyamines (PAs) are amines with low-molecular-mass positively charged at physiological pH. They can be found as free molecules or conjugated into small (such as coumaroyl, ferulic, or hydrocinnamic acids) and large molecules (such as lipids, nucleic acids, and proteins) (Minocha et al. 2014; Masson et al. 2017; de Oliveira et al. 2017). The most common PAs in plants are putrescine (Put), spermidine (Spd), and spermine (Spm) (Majumdar et al. 2016; de Oliveira et al. 2018), followed by cadaverine (Cad), and thermospermine (Cohen 1998; Minguet et al. 2008), an isomer of spermine. PAs are synthesized from the amino acids glutamate (Glu), glutamine (Gln), ornithine (Orn), and arginine (Arg) (Majumdar et al. 2016; de Oliveira et al. 2018; Jangra et al. 2023). The Glu to proline (Pro), Orn, Arg, PAs, and γ-aminobutyric acid (GABA) reactions constitute one of the major interactive pathways for carbon (C) and nitrogen (N) assimilation and partitioning (Majumdar et al. 2016; de Oliveira et al. 2018). In general, PAs are present in large amounts in cells and can scavenge N, influencing the total distribution of N in multiple pathways (Salo et al. 2016) and the N:C balance (Mattoo et al. 2006). Additionally, fluctuations in PA concentration are often related to plant responses to different stresses and growth phases (Minocha et al. 2014; Cheng et al. 2019; Sheng et al. 2022; Jangra et al. 2023). Thus, significant changes in PA biosynthesis and catabolism can affect the cellular pool of other metabolites, including amino acids, sugars, and phytohormones, such as abscisic acid (ABA) and indole-3-acetic acid (IAA) (Jangra et al. 2023).

Abscisic acid regulates several physiological functions in plants, from seed germination to stomatal movements, acting as an enhancer or repressor of plant growth and development (Chen et al. 2019b; Parwez et al. 2022). Abiotic stress conditions stimulate ABA biosynthesis leading to stress mitigation responses via modulation of gene expression, metabolism, and crosstalk with other hormones (Chen et al. 2020; Bulgakov and Koren 2022; Parwez et al. 2022). For instance, in high-temperature conditions, ABA increases the concentrations of starch, and non-structural carbohydrates (Rezaul et al. 2019; Chen et al. 2019b).

Indole-3-acetic acid is the most common auxin and plays a vital role in plant growth and development (Jangra et al. 2023). It regulates cell division, expansion and differentiation, apical dominance, embryogenic development, root and stem tropisms, and the transition to flowering (Bunsangiam et al. 2021; Jangra et al. 2023). Although auxin controls the whole plant development, its homeostasis is important for maintaining the hormonal balance at a level suitable for proper plant growth. Moreover, high concentrations of IAA can exert an inhibitory effect on plant physiological processes (Bunsangiam et al. 2021).

Amino acids act as building blocks of proteins and intermediate the biosynthesis of many compounds such as PAs (Galili et al. 2008). Under reduced nutrient availability, free amino acids and other metabolites might be released from the catabolism of macromolecules activating protein kinases such as the general nutrient sensor target of rapamycin complex 1 (TORC1), which coordinates the metabolism of sugars (Xiong et al. 2013) and N (Mubeen et al. 2018; Cao et al. 2019). This process contributes to osmotic adjustment and maintenance of the plant energy state,

establishing another cross-talk between C and N metabolism (Kohli et al. 2012; Mubeen et al. 2018).

Together, amino acids, PAs, and hormones can act in numerous processes such as leaf and flower senescence, plant architecture, development, and abiotic stress tolerance (Minocha et al. 2014; Kumar et al. 2019). Besides, these metabolites are tightly regulated and oscillate in response to environmental inputs (i.e., stress and water availability) or during the transition between different developmental stages (i.e., juvenile, adult, or senescence stages). In this way, an integrated investigation of these compounds can be used to determine the fine regulation of crop growth and development, especially in plants subjected to different environmental stimuli as those growing in the field.

Sugarcane is an important crop in Brazilian agriculture and bioenergy scenarios (De Souza et al. 2014; Cursi et al. 2022). Attention to biomass residues from sugar and biofuel industries to enhance cellulosic ethanol production for a sustainable energy future has led to scientific advances in understanding sugarcane physiology and molecular biology (De Souza et al. 2014). However, how the concentrations of PAs, IAA, ABA, and amino acids fluctuate at different phases of sugarcane development and their influence on plant growth and yield performance is unknown. In this study, we evaluated the variation in these compounds in the leaves and culms of *Saccharum* spp. cv. SP80-3280 during the crop cycle in the field.

2 Material and methods

2.1 Plant material

Plants of *Saccharum* spp. (cv. SP80–3280) were grown in a field plot measuring 2,112.5 m^2 with rows spaced at 1.4 m apart and harvested during the second ratoon cycle (De Souza et al. 2018). Fertilizer (500 kg ha^{-1} of 20:00:20 N:P:K) and herbicides (Combine 500C from Dow AgroSciences and Flumyzin 500 from Sumitomo Chemical) were applied to the clay soil at the experimental site according to the farmer's standard practices. Climate conditions (temperature, relative humidity, accumulated rainfall, and accumulated solar radiation) during the experiment are available in De Souza et al. (2018). Green fully expanded leaves (leaf + 1) and culm (mature internodes) were collected along the diurnal cycle in 01, 03, 06, and 12 months of development, frozen in liquid nitrogen, ground to a fine powder, and stored at -80 °C . Twelve biological replicates were used for each month for biochemical characterization. For quantifying IAA and ABA, eight replicates were used.

2.2 Measurement of free amino acids

Free amino acids were extracted and quantified according to de Oliveira et al. (2018). Aliquots of fresh material (10 mg of leaves and 40 mg of culms) were extracted with 80 % ethanol (v/v). Amino acids were derivatized with *o*-phthalaldehyde, separated by high-performance liquid chromatography (HPLC, Shimadzu, Japan) on a C_{18} reverse-phase column (5 µm × 4.6 mm × 250 mm—Supelcosil LC-18, Sigma-Aldrich, USA), and quantified by comparison with authentic standards: aspartate (Asp), glutamate (Glu), asparagine (Asn), serine (Ser), glutamine co-eluted with histidine (Gln + His), glycine (Gly), arginine (Arg), threonine (Thr), alanine (Ala), tyrosine co-eluted with γ-aminobutyric acid (Tyr + GABA), methionine (Met), tryptophan (Trp), valine (Val), phenylalanine (Phe), isoleucine (Ile), leucine (Leu), ornithine (Orn), lysine (Lys), and citrulline (Cit).

2.3 Analysis of free PAs

Putrescine, spermidine, cadaverine, and spermine were extracted as described by de Oliveira et al. (2018). Aliquots of fresh material (10 mg of leaves and 40 mg of culms) were homogenized with cold 5 % (v/v) perchloric acid at a ratio of 1:4 (m/v, i.e., 10 mg of tissue in 40 mL of perchloric acid) and subjected to three cycles of freezing (at −20 °C for 2h30) and thawing (at room temperature, around 2 h). Later, extracts were centrifuged at 14,000 g for 20 min at 4 °C. The supernatants containing free PAs were collected and derivatized according to Silveira et al. (2008). Extracts (40 µL) were mixed with 100 µL of dansylchloride (5 mg mL^{-1} in acetone), 20 µL of 0.05 mM diaminoheptane (internal standard), and 50 µL of saturated sodium carbonate. After 50 min of incubation in the dark at 70 °C, the excess of dansylchloride was

converted to dansylproline by adding 25 µL of proline (100 mg mL^{-1}). Subsequently, samples were incubated for 30 min at room temperature. Dansylated PAs were extracted with 200 µL of toluene and the supernatant was collected and dried under flowing nitrogen gas. Dansylated PAs were dissolved in 200 µL of acetonitrile. PAs were separated by HPLC on a reversed-phase C_{18} column (as described above) mixing increasing proportions of absolute acetonitrile with 10% acetonitrile in water (pH 3.5). The gradient of absolute acetonitrile was set to 0–65 % for the first 10 min, 65–100% from 10 to 13 min, and 100% from 13 to 21 min, at a flow rate of 1 L min^{-1} at 40 °C. PAs were detected at 340 nm (excitation) and 510 nm (emission) wavelengths with an RF-20A fluorescence detector (Shimadzu, Japan).

2.4 IAA and ABA quantification

The hormones ABA and IAA were extracted and quantified according to Silveira et al. (2008) and Álvarez-Florez et al. (2017) with modifications. Aliquots of 50 mg of the dry mass (DM) of leaves and culms were homogenized in 2.5 mL extraction buffer containing methanol and isopropanol (20:80 v/v), 1 % acetic acid (v/v), and [^{3}H]IAA and [^{3}H] ABA at a concentration of 0.5 µCi mL^{-1} (internal standards). Samples were analyzed by HPLC using the same reversed-phase C_{18} column described above. ABA and IAA concentrations were determined using a UV–VIS detector at 254 nm and a fluorescence detector at 280 nm (excitation) and 350 nm (emission), respectively.

2.5 Data analysis

Data were analyzed by the Kruskal–Wallis test or by analysis of variance (ANOVA), followed by pairwise multiple comparison procedures with different tests, described in the results. Heatmaps were performed using MetaboAnalyst version 5.0 (Pang et al. 2021).

3 Results

3.1 Total amino acids were higher at the beginning of sugarcane development

To evaluate the changes in amino acid concentrations during the development of sugarcane, samples of leaves and culms were analyzed across a 12-month growth period in the field (01, 03, 06, and 12 months) (Fig. 1). Total concentrations of amino acids decreased in both organs during development. However, a significant reduction was observed in the culm in month 03. The highest values of total amino acids for leaves and culms were found in the first month, but culms showed concentrations approximately 12-fold higher than leaves (Fig. 1A).

The 21 investigated amino acids were quantified in the culm. However, Cit was present in this tissue only during the first month of development (Fig. 1B and C and Additional file 1) and was not detected in leaves. In culm, Asn showed the highest concentrations, peaking in the first month (Additional file 1). In contrast, the more abundant amino acids in the leaf were Orn and Lys (Fig. 1C and Additional file 1).

A heatmap was generated to better visualize variations in amino acid concentrations during the sugarcane development (Fig. 1B and C). Two well-defined clusters were formed (Fig. 1B and C) and represent different groups of metabolites with similar profiles throughout leaves or culm development. In the leaf, Asp, Asn, Ser, and Met were identified at low concentrations in cluster I (Fig. 1B), while the remaining amino acids showing higher concentrations throughout the months were grouped into cluster II.

In the culm, the first cluster was composed of Met, Glu, Ser, Trp, Phe, Arg, and Tyr + GABA, with low concentrations in most months (Fig. 1C). The remaining amino acids showing high concentrations, mainly in the first month, were in the second cluster. From the third month onwards, some amino acids showed different profiles: i) amino acids with high concentrations until the last month (Asn, Asp, and Orn); ii) amino acids with intermediary concentrations (Gly, Lys, Ala, and Val); and iii) amino acids whose concentrations decreased along development (Gln + His, Ile, Thr, Leu, and Cit).

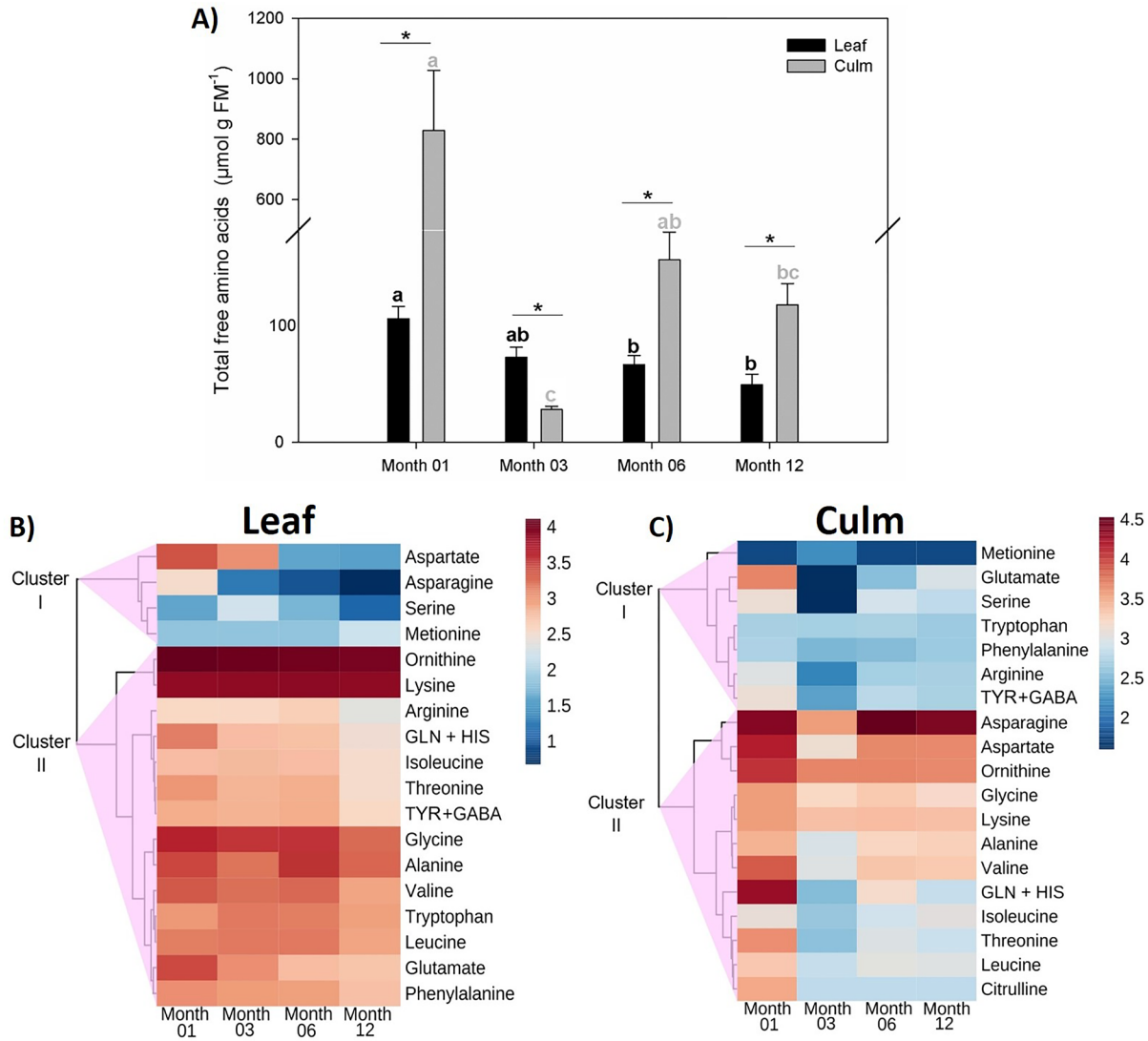

Fig. 1 Total amount of amino acids and heatmap showing amino acid variations in leaf and culm during the development of sugarcane. Total amount of amino acids (**A**) in sugarcane leaf (black bars) and culm (gray bars) throughout 12 months of development in the field. Significant differences among months (Kruskal–Wallis followed by Student–Newman–Keuls' test, $p < 0.05$) are indicated by letters whereas the difference between organs (Student's *t* test $p > 0.05$) is indicated by asterisks. Values are means ± standard error (n = 12). Heatmaps showing the variation in the amino acid concentrations in leaf (**B**) and culm (**C**) culm during the development of sugarcane. Glutamine co-eluted with histidine (Gln + His) and tyrosine co-eluted with γ-aminobutyric acid (Tyr + GABA). Data were transformed into $\log_{10}$. Samples/lines show the natural contrast between groups using the ward clustering method

3.2 Sugarcane has higher Total-PAs in leaf than in culm

Putrescine, spermidine, spermine, and cadaverine were detected in leaves and culms of sugarcane (Fig. 2). Total-PAs (sum of all identified PAs) were higher in leaves than in culm in all months analyzed (Fig. 2A and B), being 2.9- and 13.2-fold higher in months 01 and 06, respectively. In leaves, Total-PAs decreased in the last month of development (Fig. 2A), whereas this decrease was observed from the third month on in culms (Fig. 2B).

The concentrations of each PA in the leaf (Fig. 2A) and culm (Fig. 2B) revealed that putrescine (Fig. 2A)

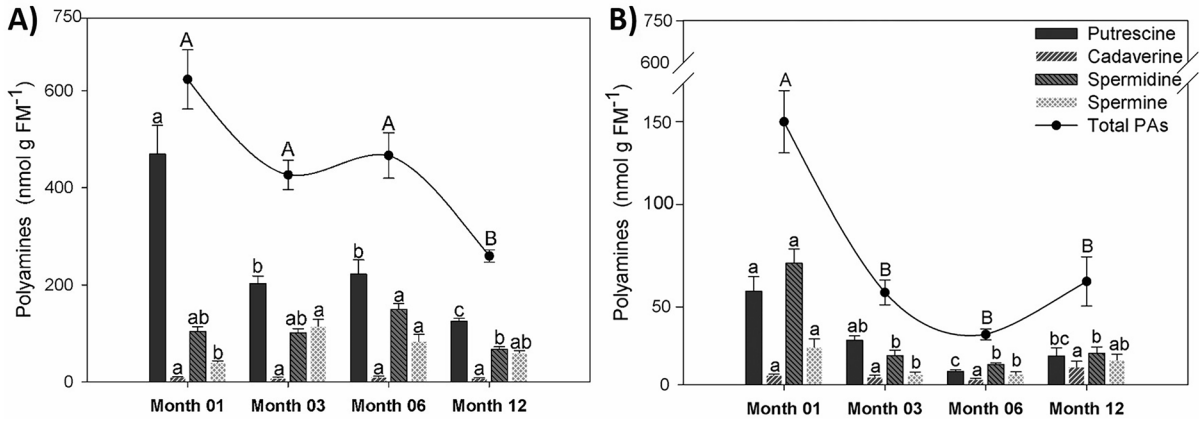

Fig. 2 Polyamine concentrations in sugarcane leaf (**A**) and culm (**B**) throughout development in the field. Bars represent the average concentration of each polyamine (PA) (putrescine, cadaverine, spermidine, and spermine) and the line is the total polyamine concentration in each month. Significant differences for each PA among months (Kruskal–Wallis followed by Tukey test, $p < 0.05$) are indicated by lowercase letters whereas the difference between the total polyamine concentration is indicated by uppercase letters. Values are means ± standard error (n = 12)

and spermidine (Fig. 2B) contributed to the higher concentrations of Total-PAs in month 01. In addition, putrescine was the main PA in the leaf along the sugarcane development, followed by spermidine and spermine. Spermidine concentrations were more constant in the leaf than in the culm. This latter had a higher spermidine concentration in the first month only. Opposite profiles were found for spermine between the two organs. In the leaf, a tendency for spermine concentrations to increase was observed during months 03 and 06, opposite to its decrease in the culm. Cadaverine showed basal amounts and no significant changes in all months for both organs (Fig. 2A and B).

3.3 High concentrations of IAA and ABA are present in leaves at the end of the sugarcane development

Sugarcane leaf and culm had different IAA and ABA profiles (Fig. 3A) during development, especially

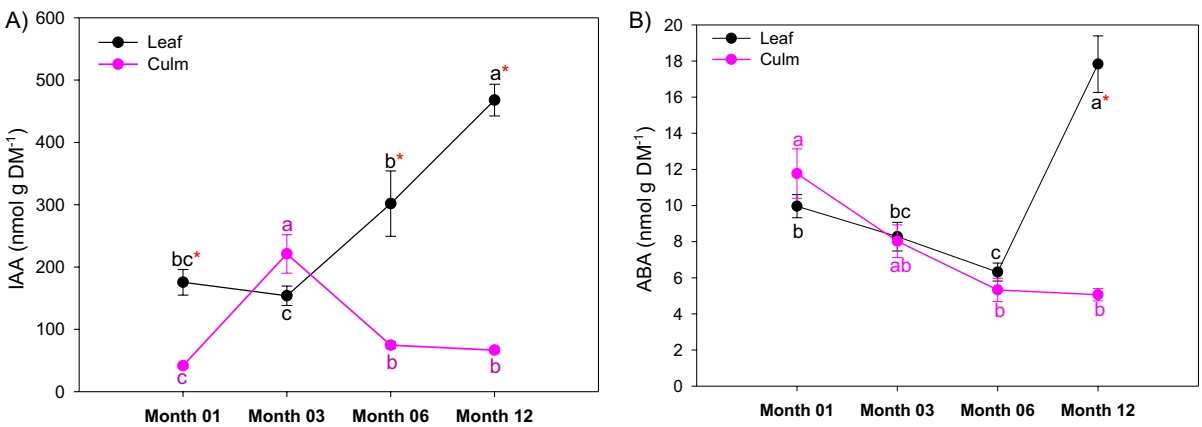

Fig. 3 Concentrations of indole-3-acetic acid (IAA) (**A**) and abscisic acid (ABA) (**B**) in leaves (black) and culms (pink) throughout sugarcane development in the field. Significant differences among months (Tukey test $p < 0.01$) are indicated by letters whereas the difference between organs (Student's t test $p < 0.01$) is indicated by asterisks. Values are means ± standard error (n = 8)

concerning the higher leaf IAA concentrations in most time points analyzed. IAA concentrations were similar between the two organs at month 03 and ninefold higher in the leaf at month 12 (Fig. 3A). In the leaf, a significant increase in the amount of IAA was detected from months 03 to 12, whereas in culm this happened between months 01 and 03.

Leaf and culm had similar concentrations of ABA during the first three months of development, and a slight decrease was observed from the first until the sixth month. At month 12, ABA concentrations were threefold higher in the leaf compared to culm (Fig. 3B).

3.4 Metabolite concentrations were overall more variable in leaves than in culms

To provide an overview of the metabolite changes during sugarcane development, we combined the data from carbohydrate quantification from De Souza et al. (2018) with the results presented here (Fig. 4). Overall, the relative amount of metabolites was more variable among the months in leaf compared to the culm. As expected, the metabolite in the highest amount in the culm and leaf was sucrose. Unlike amino acids, whose concentrations fluctuate over months, hormones were present in low amounts in all months.

4 Discussion

Carbon (C) molecules are used as energy and C-skeleton for metabolic processes and growth, which influences C partitioning and transport to different tissues during plant development (Hartman et al. 2020; Da Silva et al. 2023). The patterns of carbohydrate distribution in different metabolic pathways were recently investigated in sugarcane and energy-cane varieties (Da Silva et al. 2023), but information on other metabolites (plant hormones, polyamines, and amino acids) and their seasonal

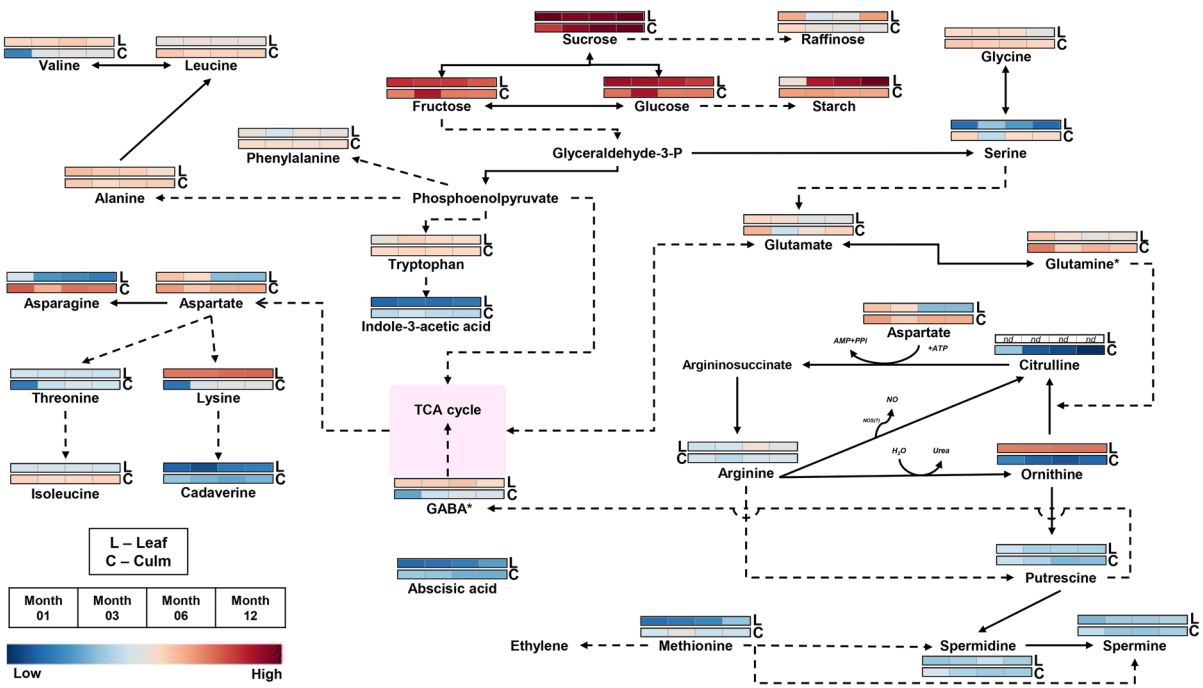

Fig. 4 Schematic overview of the changes in carbohydrate, amino acid, and polyamine metabolism throughout sugarcane development in the field. Changes in metabolite accumulation in leaf (L) and culm (C) are indicated by heatmaps generated separately for each organ. The solid lines indicate direct conversion and the dashed lines indirect conversion. Asterisks indicate that glutamine co-eluted with histidine and tyrosine co-eluted with γ-aminobutyric acid (GABA). Red and blue indicate high and low metabolite concentrations, respectively. Data regarding carbohydrates (glucose, fructose, sucrose, raffinose, and starch) were originally published by De Souza et al. (2018)

fluctuations are usually overlooked. A broader understanding of how nonstructural carbohydrates are built, used, and stored, as well as other metabolites could shed light on how these compounds are regulated during sugarcane development.

4.1 Increasing amino acid concentrations is correlated with enhanced sugarcane biomass production

Plant growth and development are fueled by primary metabolism, which includes the synthesis, use, and accumulation of carbohydrates, amino acids, and lipids. Together with hormones, these compounds regulate various physiological, biochemical, and molecular processes (Paul and Pellny 2003; De Souza et al. 2018). For instance, sugars are the primary energy source and provide the necessary building blocks for biomass production. Amino acids derived from sugar metabolism and external sources, play a crucial role in protein synthesis and interact with hormones influencing their biosynthesis (Galili et al. 2008). The interplay between these metabolites is particularly evident in stress responses, where sugars and amino acids, as well as PAs, act as osmoprotectants and signaling molecules, coordinating stress adaptation through the modulation of hormone concentrations (see reviews Minocha et al. 2014; Sami et al. 2016). However, how these metabolites contribute synergistically to biomass production remains elusive. This is particularly relevant for agronomically important traits.

In sugarcane, information about amino acid metabolism throughout the development is scarce. Wiggins and Williams (1955) detected 11 amino acids in leaves and culms of 12 sugarcane varieties and identified a decrease in their concentrations during sugarcane development, as we also observed (Fig. 1). Da Silva et al. (2023) identified 14 amino acids and the polyamine putrescine in the leaf and culm of sugarcane (RB867515) and energy cane (Vertix 8) varieties. Together, the fluctuations in amino acids, putrescine (Da Silva et al. 2023), and carbohydrates (De Souza et al. 2018) concentrations impact the metabolism of distinct sugarcane varieties. The patterns of metabolite variation seem to be determined by several factors, such as environmental conditions and the source-sink relationship. In sugarcane, the culm is a robust sink and accumulates more than 55% of its dry mass in the form of sucrose (Waclawovsky et al. 2010). However, this organ becomes a source when cuttings containing axillary buds are used for vegetative propagation. In this phase, culm supplies C and other nutrients for bud sprouting and root formation (Boussiengui-Boussiengui et al. 2016).

Here, we measured a larger number of amino acids in comparison to previous works and found a high concentration of total free amino acids in sugarcane culms in the first month of development (Fig. 1A). As we analyzed sugarcane plants from the second ratoon cycle, possibly this high accumulation occurs because the culm is under a sink-to-source transition. In addition, the formation of new shoots after the harvest depends on the expansion of a new root system, but old roots are still active for several weeks (Ball-Coelho et al. 1992) and the sucrose stored in the culms might function as a reserve to maintain their metabolism (De Souza et al. 2018). Isotopic analysis in the sugarcane variety NA 56–79 N has revealed that reserves from the culms are important for seedling establishment in the first 50–60 days of development (Carneiro et al. 1995). In this sense, sugars and amino acids support the growth and development of the aerial part during the sink-to-source transition.

The amino acids more abundant in culm and leaves were Gln, Asn, Asp, Glu, and Orn, which are related to the PA biosynthetic pathway (Fig. 4). The high concentration of PAs, mainly putrescine, suggests a high demand for these amino acids (Majumdar et al. 2013, 2017).

4.2 Asn, Lys, and Orn can influence how sugarcane deals with environmental adversities and N assimilation

New insights into the regulation of metabolic networks among tissues can be obtained through the investigation of the connectivity and abundance of amino acids, as well as the correlation between amino acids and other metabolites (Ferreira et al. 2018). The amino acids clustered according to their changes in abundance during sugarcane development (Fig. 1B-C). In the leaf, cluster I is composed of amino acids with low abundance during development such as Ser, Met, and Asn (Fig. 1B). Asparagine showed the most distinct profile in comparison to the other

metabolites in both organs, with high concentration in the first month (Fig. 1B and Fig. 4). Asparagine is an N-rich amino acid and often associated to transport and storage of N. In addition, Asn is a water-stress responsive metabolite in plants and is present in the large concentration in sugarcane (Wiggins and Williams 1955; Iskandar et al. 2011). Its synthesis occurs by deamination and transamination processes, which release N for the synthesis of other amino acids and proteins (Kurmi and Haigis 2020) mainlyat high energetic demand phases.

Da Silva (2023) showed that diurnal variations in Asn and Lys in the leaf of sugarcane are associated with the C supply, whereas Orn was differentially significant only in the internode. In our study, Lys and Orn were present in high concentrations in the leaf in all months (Fig. 2A and Additional File 1). Lys concentration increases during drought, osmotic, and salt stress due to protein hydrolysis, inducing the transcriptional regulation of genes involved in the saccharopine pathway (that converts Lys to α-aminoadipate) and the use of Glu to produce Pro (Arruda et al. 2000; Arruda and Barreto 2020). Transgenic *Arabidopsis* constitutively overexpressing an N-acetyl-L-glutamate synthase gene have a high concentration of Orn in the leaves, which leads to a higher tolerance to drought stress compared to wild-type plants (Kalamaki et al. 2009a,b). Additionally, Orn can serve as a precursor for PAs via the enzyme ornithine decarboxylase (Majumdar et al. 2013; Winter et al. 2015) and regulate an entire subset of pathways for Glu, Arg, and Pro (Majumdar et al. 2013), important for abiotic stress tolerance and the regulation of N assimilation (Marco et al. 2011; Gupta et al. 2013).

4.3 PAs, IAA, and ABA may be associated with protection against abiotic stress and senescence in sugarcane

Plant growth and development are controlled by endogenous and exogenous cues. PAs show tissue- and organ-specific distribution patterns (Chen et al. 2019a), and there seems to exist a link between sugar metabolism, PAs, IAA, and ABA (Bai et al. 2021). In general, the most abundant PAs in plants are putrescine (leaves) and spermidine (other organs) (Takahashi et al. 2018). This same profile was detected in month 01 in sugarcane (Fig. 2A and B), in which putrescine concentrations were 2.6 times higher in the leaf. Putrescine was the PA more abundant in leaves in all months of development. Putrescine interacts with various regulatory molecules and/or regulates the expression of different genes such as those involved in ABA and IAA biosynthesis (González-Hernández et al. 2022). In addition, putrescine can modulate chlorophyll concentrations but how this happens is unclear (for review see González-Hernández et al. 2022). Wheat plants treated with exogenous putrescine accumulate higher total carbohydrate concentrations due to the stimulation of photosynthetic CO_2 assimilation (El-Bassiuony and Bekheta El-Bassiouny et al. 2008; Ioannidis et al. 2012). Increased carbohydrate concentrations were also observed in sugarcane leaves from 03 months onwards (De Souza et al. 2018).

Ripening or senescence starts after a certain physiological age and involves a series of changes at the physiological, biochemical, and molecular levels. Pandey et al. (2000) demonstrated the involvement of PAs and the hormone ethylene in this process. Both have a common precursor in their biosynthetic pathways, *S*-adenosylmethionine (SAM) (Majumdar et al. 2017). Although SAM is preferentially transformed into PAs (Khan and Singh 2010), competition between the biosynthesis of PAs and ethylene might occur. All PAs showed lower concentrations in leaf and culm in the last month (12) of development (Fig. 4) when leaf senescence reached 40% of the canopy (De Souza et al. 2018). Therefore, SAM may be directing the flux towards ethylene synthesis to promote senescence. Additionally, ABA and ethylene interact antagonistically and/or influence each other's synthesis and their signaling transduction pathways (Müller 2021). In our study, higher concentrations of ABA were found in leaves at month 12, which can also be associated with senescence. Although we have not measured ethylene concentration in this study, its biosynthesis might be induced by higher ABA or by decreased PA biosynthesis as demonstrated in different plants (Zhang et al. 2009; Mou et al. 2016; Zhao et al. 2016). In this sugarcane experiment, leaves from the bottom canopy started to senesce at 6 months and senescence increased up to 12 months (De Souza et al. 2018), in agreement with the hormonal profiles observed in the present study (Fig. 4 and 5).

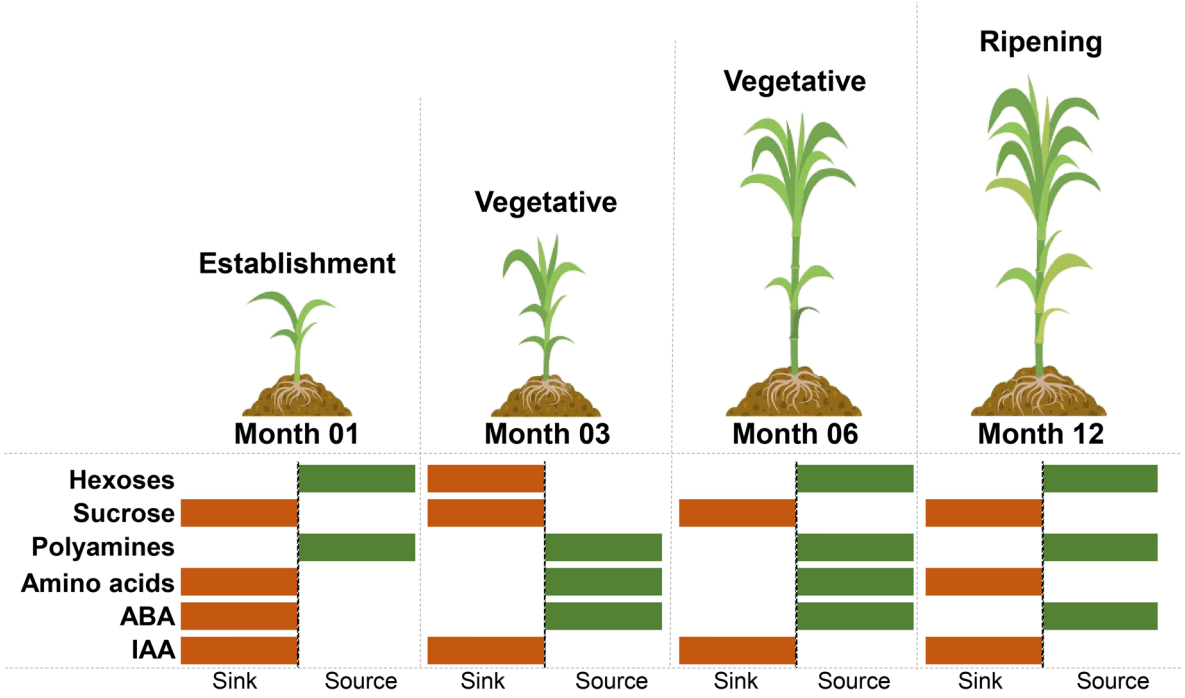

Fig. 5 Phenological stages of sugarcane development in the field indicate variations in the source/sink strength. In the first month, plants are establishing stage; in the third month, plants have already reached the vegetative stage, being ready for harvest at the twelfth month of cultivation (ripening). The ratio of the total concentrations of hexoses (glucose and fructose), sucrose, PAs, amino acids, ABA, and IAA between the leaf and the culm for each month was used to calculate source (green) and sink (orange) strength. Data regarding hexoses and sucrose were originally published by De Souza et al. 2018

Hormones such as auxin, ABA, cytokinin, salicylic acid, gibberellic acid, ethylene, brassinosteroids, and jasmonic acid play a pivotal role in sucrose biosynthesis and accumulation in sugarcane (for review see Misra et al. 2022). Here, we found that the concentrations of IAA increased in expanded leaves from the 6th month onwards, peaking at the 12th month, which coincides with the final development of sugarcane. Auxin plays central roles in leaf development, including leaf initiation, blade formation, and compound leaf patterning (Xiong and Jiao 2019). In *Arabidopsis*, elevation of leaf auxin concentrations has been consistently found to inhibit leaf expansion (Keller et al. 2011). Auxin also shows a crosstalk with other hormones such as ABA, ethylene, cytokinins, brassinosteroids, polyamines, and other metabolites, such as carbohydrates and amino acids (Misra et al. 2022). Auxin can stimulate the production of ethylene by influencing the transcription of certain genes and altering their expression patterns (Zemlyanskaya et al. 2018). Additionally, the presence of specific regulatory elements in gene promoters suggests a coordinated interaction between PAs, auxin, and ethylene during the growth and development of plants (Majumdar et al. 2017). Similarly, Chen et al. (2019b) have found that the interaction of phytohormones particularly ethylene, ABA, and other sugar molecules helps to modify the production and storage of sucrose. Ethylene activates genes linked with the metabolic activities of carbohydrates like sucrose synthase and invertases that presumably enhance the potential of sink strength and the efficiency of sucrose unloading from the phloem (Misra et al. 2022). In this context, the intrinsic interplay of plant hormones enables the plant to perform specific physiological functions at both spatial and temporal levels. Studying hormone-hormone or hormone-metabolic interactions is a highly competitive field of research aimed at unraveling the underlying regulatory mechanisms, however, in sugarcane, more studies are necessary.

4.4 PAs, amino acids, auxin, and sucrose: possible crosstalks?

An interaction among sugar, amino acids, and PAs metabolism was previously demonstrated by the application of exogenous sucrose (Altuntaş et al. 2019), which regulated genes involved in PAs synthesis and increased concentrations of Pro and PAs in maize seedlings exposed to drought (Altuntaş et al. 2019). Additionally, PAs increase both the photosynthetic rate in flag leaves and carbohydrate accumulation, thereby promoting grain filling in wheat (Liu et al. 2013). Application of spermidine in *Vitis vinifera* increased soluble sugar concentrations, mainly sucrose, but reduced amino acids in leaves, evidencing that sucrose and amino acids displayed opposite tendencies influenced by PAs (Aziz 2003). Interestingly, the sucrose accumulation profile (De Souza et al. 2018) in leaf and culm appears to be inverse to amino acid accumulation and displays a negative correlation in all months in leaves and in the first month in the culm (Additional file 2). This correlation was also observed in a metabolome analysis performed during culm development (Glassop et al. 2007) and in sugarcane suspension cells (Wendler et al. 1991; Veith and Komor 1993).

Our results indicate an interrelation between the accumulation of sugars and other metabolites, such as amino acids, PAs, and hormones in the sugarcane source (leaves) and sink (culm) organs (Fig. 5). The strength of source-sink targeting, an approach adapted from Benning et al. (2023), revealed that sucrose and IAA concentrations increase sink strength, while PAs concentrations increase the source strength during the 3–6-month transition. During this transition, carbohydrates start to accumulate in culms, mainly sucrose, along with the downregulation of photosynthesis and growth (De Souza et al. 2018). In addition, this high concentration of IAA in the culm during the 3rd month may be related to the need for the culm to grow. In Moso bamboo, shoot tips have the highest auxin concentrations and may be the main site of auxin biosynthesis in the early stage of rapid growth (Bai et al. 2022). Auxins have an indirect role in photosynthesis through the modulation of chloroplast development, stomata patterning, and leaf venation (Müller and Munné-Bosch 2021). In addition, transcription factors that respond to auxin concentration, such as auxin response factors (ARFs), have been reported to be associated with the photosynthesis ratio, as well as the accumulation of starch and soluble sugars in tomato (Yuan et al. 2019). A member of the ARF family (*ARF6A*) may be directly bound to the *SAMS1* promoter, resulting in a negative expression regulation, decreasing SAM and regulating the biosynthesis of spermidine, spermine, and ethylene (Yuan et al. 2019). Thus, our results along with those reported by De Souza et al. (2018) suggest that not only sugar concentrations, but also IAA may be associated with the regulation of hormone pathways, growth, photosynthesis, and biomass.

The amino acid concentrations also showed the sink-to-source transition in culms and leaves. Amino acids are suggested to have a regulatory role in sucrose storage, as cells only pass from the growth stage to the sucrose storage stage due to amino acid depletion and transport (Stein & Granot 2019; Kim et al. 2021). Interestingly, genotypes of sugarcane with higher sprouting rates tend to have higher concentrations of putrescine, whereas genotypes with low sprouting rates show higher concentrations of sugars and amino acids (Ferreira et al. 2018). Considering this, amino acids and PA might have a relationship with sucrose accumulation during the substantial transition period (growth *vs*. accumulation). However, more functional studies are needed to validate this interaction.

5 Conclusions

PAs, IAA, and ABA can be involved with senescence, and the high metabolism of amino acids in the culm appears to play a vital role in maintaining the energy balance of sugarcane, providing the essential resources to support plant establishment and survival. Together, these fluctuations indicate metabolic specificities of each organ throughout development and pave the way for a more integrative understanding of the biological functioning of sugarcane in the field, which can lead to future strategies to improve yield performance.

Acknowledgements We acknowledge the University of São Paulo, the National Council for Scientific and Technological Development (CNPq), and the São Paulo Research Foundation (FAPESP) for supporting this study.

Author contributions LPO and MSB conceived the study. Material preparation and data collection were performed by LPO and AFM. LPO, LFO, and BVN carried out analyses and interpreted the data. The first draft of the manuscript was written by LPO and LFO, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding This work was supported by the National Institute of Bioethanol Science and Technology—INCT of Bioethanol (FAPESP 2014/50884–5 and CNPq 465319/2014–9) and the Research Center of Green House Gas Innovation (RCGI) (FAPESP 2014/50279–4 and 2020/15230–5). LPO (CNPq 142090/2018–2 and RCGI 371055), LFO (RCGI 371055, FAPESP 2024/12357-5), BVN (FAPESP 2022/00441–6), EISF (CNPq 307315/2022–3), and MCMM (FAPESP 2018/03764–5) are grateful for their fellowships.

Data availability All data supporting the findings of this study are included in the paper.

Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

References

Alcázar R, Altabella T, Marco F, Bortolotti C, Reymond M, Koncz C, Carrasco P, Tiburcio AF (2010) Polyamines: molecules with regulatory functions in plant abiotic stress tolerance. Planta 2010(231):1237–1249

Altuntaş C, Sezgin A, Demiralay M, Terzi R, Sağlam A, Kadioğlu A (2019) Application of sucrose modulates the expressions of genes involved in proline and polyamine metabolism in maize seedlings exposed to drought. Biol Plant 63:247–252. https://doi.org/10.32615/bp.2019.028

Álvarez-Flórez F, López-Cristoffanini C, Jáuregui O, Melgarejo LM, López-Carbonell M (2017) Changes in ABA, IAA and JA levels during calyx, fruit and leaves development in cape gooseberry plants (*Physalis peruviana* L.). Plant Physiol Biochem 115:174–182. https://doi.org/10.1016/j.plaphy.2017.03.024

Anwar R, Mattoo AK, Handa AK (2000) Polyamine interactions with plant hormones: crosstalk at several levels. in polyamines; Springer: Tokyo. Japan 2015:267–302

Arruda P, Barreto P (2020) Lysine catabolism through the saccharopine pathway: enzymes and intermediates involved in plant responses to abiotic and biotic stress. Front Plant Sci 11:535796. https://doi.org/10.3389/fpls.2020.00587

Arruda P, Kemper EL, Papes F, Leite A (2000) Regulation of lysine catabolism in higher plants. Trends Plant Sci 5(8):324–330. https://doi.org/10.1016/s1360-1385(00)01688-5

Aziz A (2003) Spermidine and related-metabolic inhibitors modulate sugar and amino acid levels in *Vitis vinifera* L.: possible relationships with initial fruitlet abscission. J Exp Bot 54(381):355–363. https://doi.org/10.1093/jxb/erg029

Bai Q, Huang Y, Shen Y (2021) The physiological and molecular mechanism of abscisic acid in regulation of fleshy fruit ripening. Front Plant Sci 11:619953. https://doi.org/10.3389/fpls.2020.619953

Bai Y, Cai M, Mu C, Cheng W, Zheng H, Cheng Z, Li J, Mu S, Gao J (2022) New insights into the local auxin biosynthesis and its effects on the rapid growth of moso bamboo (*Phyllostachys edulis*). Front Plant Sci 13:858686. https://doi.org/10.3389/fpls.2022.858686

Ball-Coelho B, Sampaio EVSB, Tiessen H (1992) Stewart JWB (1992) root dynamics in plant and ratoon crops of sugar cane. Plant Soil 142:297–305. https://doi.org/10.1007/BF00010975

Benning UF, Chen L, Watson-Lazowski A, Henry C, Furbank RT (2023) Ghannoum O (2023) spatial expression patterns of genes encoding sugar sensors in leaves of C4 and C3 grasses. Ann Bot 131(6):985–1000. https://doi.org/10.1093/aob/mcad057

Botha FC, Lakshmanan P, O'Connell A, Moore PH (2013) Hormones and Growth Regulators (331–377). In Sugarcane: Physiology, Biochemistry, and Functional Biology (eds PH Moore and FC Botha). Wiley Online Library. https://doi.org/10.1002/9781118771280.ch14.

Boussiengui-Boussiengui G, Groenewald JH, Botha FC (2016) Metabolic changes associated with the sink-source transition during sprouting of the axillary buds on the sugarcane culm. Tropical Plant Biol 9:1–11. https://doi.org/10.1007/s12042-015-9158-8

Bulgakov VP, Koren OG (2022) Basic protein modules combining abscisic acid and light signaling in *Arabidopsis*. Front Plant Sci 12:808960. https://doi.org/10.3389/fpls.2021.808960

Bunsangiam S, Thongpae N, Limtong S, Srisuk N (2021) Large scale production of indole-3-acetic acid and evaluation of the inhibitory effect of indole-3-acetic acid on weed growth. Sci Rep 11:13094. https://doi.org/10.1038/s41598-021-92305-w

Caldana C, Martins MCM, Mubeen U, Urrea-Castellanos R (2019) The magic 'hammer' of TOR: the multiple faces of a single pathway in the metabolic regulation of plant growth and development. J Exp Bot 70(8):2217–2225. https://doi.org/10.1093/jxb/ery459

Cao P, Kim S, Xing A, Schenck CA, Liu L, Jiang N, Wang J, Last RL, Brandizzi F (2019) Homeostasis of branched-chain amino acids is critical for the activity of TOR signaling in *Arabidopsis*. Elife. https://doi.org/10.7554/eLife.50747

Carneiro AEV, Trivelin PCO, Victoria RL (1995) Utilization of the organic and nitrogen reserve of the seed piece by the cane plant. Scientia Agricola 52:199–209

Chen D, Shao Q, Yin L, Younis A, Zheng B (2019a) Polyamine function in plants: metabolism, regulation on development, and roles in abiotic stress responses. Front Plant Sci 9:1945. https://doi.org/10.3389/fpls.2018.01945

Chen T, Li G, Islam MR, Fu W, Feng B, Tao L, Fu G (2019b) Abscisic acid synergizes with sucrose to enhance grain yield and quality of rice by improving the source-sink relationship. BMC Plant Biol 19(1):525. https://doi.org/10.1186/s12870-019-2126-y

Chen K, Li GJ, Bressan RA, Song CP, Zhu JK, Zhao Y (2020) Abscisic acid dynamics, signaling, and functions in plants. J Integr Plant Biol 62(1):25–54. https://doi.org/10.1111/jipb.12899

Cohen SS (1998) A guide to the polyamines. Oxford University Press, New York

Cursi DE, Hoffmann HP, Barbosa GVS, Bressiani JA, Gazaffi R, Chapola RG, Fernandes Junior AR, Balsalobre TWA, Diniz CA, Santos JM, Carneiro MS (2022) History and current status of sugarcane breeding, germplasm development and molecular genetics in Brazil. Sugar Tech 24:112–133. https://doi.org/10.1007/s12355-021-00951-1

Da Silva JJB, de Abreu LGF, Ferrari AJR, de Carvalho LM, Grandis A, Buckeridge MS, Fill TP, Pereira GAG, Carazzolle MF (2023) Diurnal metabolismo of energy-cane and sugarcane: a metabolomic and non-structural carbohydrate analysis. Ind Crops Prod 202:117056. https://doi.org/10.1016/j.indcrop.2023.117056

de Oliveira LF, Elbl P, Navarro BV, Macedo AF, dos Santos ALW, Floh EIS (2017) Elucidation of the polyamine biosynthesis pathway during Brazilian pine (*Araucaria angustifolia*) seed development. Tree Physiol 37(1):116–130. https://doi.org/10.1093/treephys/tpw107

de Oliveira LF, Navarro BV, Cerruti GV, Elbl P, Minocha R, Minocha SC, dos Santos ALW, Floh EIS (2018) Polyamine- and amino acid-related metabolism: the roles of arginine and ornithine are associated with the embryogenic potential. Plant Cell Physiol 59(5):1084–1098. https://doi.org/10.1093/pcp/pcy049

De Souza AP, Grandis A, Leite DCC, Buckeridge MS (2014) Sugarcane as a bioenergy source: history, performance, and perspectives for second-generation bioethanol. Bioenerg Res 7:24–35. https://doi.org/10.1007/s12155-013-9366-8

De Souza AP, Grandis A, Arenque-Musa BC, Buckeridge MS (2018) Diurnal variation in gas exchange and nonstructural carbohydrates throughout sugarcane development. Funct Plant Biol 45(8):865–876. https://doi.org/10.1071/FP17268

El-Bassiouny HM, Mostafa HA, El-Khawas SA, Hassanein RA, Khalil SI (2008) Abd El-monem AA (2008) physiological responses of wheat plant to foliar treatments with arginine or putrescine. Aust J Basic Appl Sci 2:1390–1403

Emenecker RJ, Strader LC (2020) Auxin-abscisic acid interactions in plant growth and development. Biomolecules 10(2):281. https://doi.org/10.3390/biom10020281

Ferreira DA, Martins MCM, Cheavegatti-Gianotto A, Carneiro MS, Amadeu RR, Aricetti JA, Wolf LD, Hoffmann HP, de Abreu LGF, Caldana C (2018) Metabolite profiles of sugarcane culm reveal the relationship among metabolism and axillary bud outgrowth in genetically related sugarcane commercial cultivars. Front Plant Sci 9:857. https://doi.org/10.3389/fpls.2018.00857

Galili S, Amir R, Galili G (2008) Genetic Engineering of Amino Acid Metabolism in Plants. In: Advances in Plant Biochemistry and Molecular Biology. Bioengineering and Molecular Biology of Plant Pathways. [s.l.] Pergamon, v. 1p. 49–80.

Glassop D, Roessner U, Bacic A, Bonnett GD (2007) Changes in the sugarcane metabolome with stem development. Are they related to sucrose accumulation? Plant Cell Physiol. 48(4): 573–84. https://doi.org/10.1093/pcp/pcm027.

González-Hernández AI, Scalschi L, Vicedo B, Marcos-Barbero EL, Morcuende R, Camañes G (2022) Putrescine: a key metabolite involved in plant development, tolerance and resistance responses to stress. Int J Mol Sci 23:2971. https://doi.org/10.3390/ijms23062971

Gupta K, Dey A, Gupta B (2013) Plant polyamines in abiotic stress responses. Acta Physiol Plant 35:2015–2036. https://doi.org/10.1007/s11738-013-1239-4

Hartman H, Bahn M, Carbone M, Richardson AD (2020) Plant carbon allocation in a changing world–challenges and progress: introduction to a Virtual Issue on carbon allocation. New Phytol 227:981–988. https://doi.org/10.1111/nph.16757

Hong J, Yang L, Zhang D, Shi J (2016) Plant metabolomics: an indispensable system biology tool for plant science. Int J Mol Sci 17(6):767. https://doi.org/10.3390/ijms17060767

Ioannidis NE, Cruz JA, Kotzabasis K, Kramer DM (2012) Evidence that putrescine modulates the higher plant photosynthetic proton circuit. PLoS ONE 7(1):e29864. https://doi.org/10.1371/journal.pone.0029864

Iskandar HM, Casu RE, Fletcher AT, Schmidt S, Xu J, Maclean DJ, Manners JM, Bonnett GD (2011) Identification of drought-response genes and a study of their expression during sucrose accumulation and water deficit in sugarcane culms. BMC Plant Biol 11:12. https://doi.org/10.1186/1471-2229-11-12

Jangra A, Chaturvedi S, Kumar N, Singh H, Sharma V, Thakur M, Tiwari S, Chhokar V (2023) Polyamines: the gleam of next-generation plant growth regulators for growth, development, stress mitigation, and hormonal crosstalk in plants—a Systematic review. J Plant Growth Regul 42:5167–5191. https://doi.org/10.1007/s00344-022-10846-4

Kalamaki MS, Alexandrou D, Lazari D, Merkouropoulos G, Fotopoulos V, Pateraki I, Aggelis A, Carrillo-López A, Rubio-Cabetas MJ, Kanellis AK (2009a) Over-expression of a tomato *N*-acetyl-L-glutamate synthase gene (*SlNAGS1*) in *Arabidopsis thaliana* results in high ornithine levels and increased tolerance in salt and drought stresses. J Exp Bot 60(6):1859–1871. https://doi.org/10.1093/jxb/erp072

Kalamaki MS, Merkouropoulos G, Kanellis AK (2009b) Can ornithine accumulation modulate abiotic stress tolerance in *Arabidopsis*? Plant Signal Behav 4(11):1099–1101. https://doi.org/10.4161/psb.4.11.9873

Keller CP, Grundstad ML, Evanoff MA, Keith JD, Lentz DS, Wagner SL, Culler AH, Cohen JD (2011) Auxin-induced leaf blade expansion in *Arabidopsis* requires both wounding and detachment. Plant Signal Behav 6(12):1997–2007. https://doi.org/10.4161/psb.6.12.18026

Khan AS, Singh Z (2010) Pre-harvest application of putrescine influences Japanese plum fruit ripening and quality. Food Sci Technol Int 16(1):53–64. https://doi.org/10.1177/1082013209353242

Kim JY, Loo EP, Pang TY, Lercher M, Frommer WB, Wudick MM (2021) Cellular export of sugars and amino acids: role in feeding other cells and organisms. Plant Physiol 187(4):1893–1914. https://doi.org/10.1093/plphys/kiab228

Kohli A, Narciso JO, Miro B, Raorane M (2012) Root proteases: reinforced links between nitrogen uptake and mobilization and drought tolerance. Physiol Plant 145(1):165–179. https://doi.org/10.1111/j.1399-3054.2012.01573.x

Kumar M, Kesawat MS, Ali A, Lee SC, Gill SS, Kim AHU (2019) Integration of abscisic acid signaling with other signaling pathways in plant stress responses and development. Plants (Basel) 8(12):592. https://doi.org/10.3390/plants8120592

Kurmi K, Haigis MC (2020) Nitrogen metabolism in cancer and immunity. Trends Cell Biol 30(5):408–424. https://doi.org/10.1016/j.tcb.2020.02.005

Li L, Sheen J (2016) Dynamic and diverse sugar signaling. Curr Opin Plant Biol 33:116–125. https://doi.org/10.1016/j.pbi.2016.06.018

Liu Y, Gu D, Wu W, Wen X, Liao Y (2013) The relationship between polyamines and hormones in the regulation of wheat grain filling. PLoS ONE 8(10):e78196. https://doi.org/10.1371/journal.pone.0078196

Majumdar R, Shao L, Minocha R, Long S, Minocha SC (2013) Ornithine: the overlooked molecule in the regulation of polyamine metabolism. Plant Cell Physiol 54(6):990–1004. https://doi.org/10.1093/pcp/pct053

Majumdar R, Barchi B, Turlapati SA, Gagne M, Minocha R, Long S, Minocha SC (2016) Glutamate, ornithine, arginine, proline, and polyamine metabolic interactions: the pathway is regulated at the post-transcriptional level. Front Plant Sci 7:78. https://doi.org/10.3389/fpls.2016.00078

Majumdar R, Shao L, Turlapati SA, Minocha SC (2017) Polyamines in the life of *Arabidopsis*: profiling the expression of S-adenosylmethionine decarboxylase (SAMDC) gene family during its life cycle. BMC Plant Biol 17(1):264. https://doi.org/10.1186/s12870-017-1208-y

Marco F, Alcázar R, Tiburcio AF, Carrasco P (2011) Interactions between polyamines and abiotic stress pathway responses unraveled by transcriptome analysis of polyamine overproducers. OMICS 15(11):775–781. https://doi.org/10.1089/omi.2011.0084

Masson PH, Takahashi T, Angelini R (2017) Editorial: molecular mechanisms underlying polyamine functions in plants. Front Plant Sci 8:14. https://doi.org/10.3389/fpls.2017.00014

Mattoo AK, Sobolev AP, Neelam A, Goyal RK, Handa AK, Segre AL (2006) Nuclear magnetic resonance spectroscopy-based metabolite profiling of transgenic tomato fruit engineered to accumulate spermidine and spermine reveals enhanced anabolic and nitrogen-carbon interactions. Plant Physiol 142(4):1759–1770. https://doi.org/10.1104/pp.106.084400

Minguet EG, Vera-Sirera F, Marina A, Carbonell J, Blázquez MA (2008) Evolutionary diversification in polyamine biosynthesis. Mol Biol Evol 25(10):2119–2128. https://doi.org/10.1093/molbev/msn161

Minocha R, Majumdar R, Minocha SC (2014) Polyamines and abiotic stress in plants: a complex relationship. Front Plant Sci 5:175. https://doi.org/10.3389/fpls.2014.00175

Misra V, Mall AK, Ansari SA, Ansari MI (2022) Sugar Transporters, sugar-metabolizing enzymes, and their interaction with phytohormones in sugarcane. J Plant Growth Regul. https://doi.org/10.1007/s00344-022-10778-z

Mou W, Li D, Bu J, Jiang Y, Khan ZU, Luo Z, Mao L, Ying T (2016) Comprehensive analysis of ABA effects on ethylene biosynthesis and signaling during tomato fruit ripening. PLoS ONE 11(4):e0154072. https://doi.org/10.1371/journal.pone.0154072

Mubeen U, Jüppner J, Alpers J, Hincha DK, Giavalisco P (2018) Target of rapamycin inhibition in *Chlamydomonas reinhardtii* triggers de novo amino acid synthesis by enhancing nitrogen assimilation. Plant Cell 30(10):2240–2254. https://doi.org/10.1105/tpc.18.00159

Müller M (2021) Foes or friends: ABA and ethylene interaction under abiotic stress. Plants (Basel) 10(3):448. https://doi.org/10.3390/plants10030448

Müller M, Munné-Bosch S (2021) Hormonal impact on photosynthesis and photoprotection in plants. Plant Physiol 185(4):1500–1522. https://doi.org/10.1093/plphys/kiaa119

Pandey S, Ranade SA, Nagar PK, Kumar N (2000) Role of polyamines and ethylene as modulators of plant senescence. J Biosci 25(3):291–299. https://doi.org/10.1007/BF02703938

Pang Z, Chong J, Zhou G, Morais DAL, Chang L, Barrette M, Gauthier C, Jacques PE, Li S, Xia J (2021) MetaboAnalyst 5.0: narrowing the gap between raw spectra and functional insights. Nucl Acids Res 49(W1):W388–W396. https://doi.org/10.1093/nar/gkab382

Parwez R, Aftab T, Gill SS, Naeem M (2022) Abscisic acid signaling and crosstalk with phytohormones in regulation of environmental stress responses. Environ Exp Bot 199:104885. https://doi.org/10.1016/j.envexpbot.2022.104885

Paul MJ, Pellny TK (2003) Carbon metabolite feedback regulation of leaf photosynthesis and development. J Exp Bot 54(382):539–547. https://doi.org/10.1093/jxb/erg052

Rezaul IM, Baohua F, Tingting C, Weimeng F, Caixia Z, Longxing T, Guanfu F (2019) Abscisic acid prevents pollen abortion under high-temperature stress by mediating sugar metabolism in rice spikelets. Physiol Plant 165(3):644–663. https://doi.org/10.1111/ppl.12759

Salo HM, Sarjala T, Jokela A, Häggman H, Vuosku J (2016) Moderate stress responses and specific changes in polyamine metabolism characterize *Scots pine* somatic embryogenesis. Tree Physiol 36(3):392–402. https://doi.org/10.1093/treephys/tpv136

Sami F, Yusuf M, Faizan M, Faraz A, Hayat S (2016) Role of sugars under abiotic stress. Plant Physiol Biochem 109:54–61. https://doi.org/10.1016/j.plaphy.2016.09.005

Sheng S, Wu C, Xiang Y, Pu W, Duan S, Huang P, Cheng X, Gong Y, Liang Y, Liu L (2022) Polyamine: a potent ameliorator for plant growth response and adaption to abiotic stresses particularly the ammonium stress antagonized by urea. Front Plant Sci 13:783597. https://doi.org/10.3389/fpls.2022.783597

Silveira V, Santa-Catarina C, Balbuena TS, Moraes FMS, Ricart CAO, Sousa MV, Guerra MP, Handro W, Floh EIS (2008) Endogenous abscisic acid and protein contents during seed development of *Araucaria angustifolia*.

Biol Plant 52:101–104. https://doi.org/10.1007/s10535-008-0018-3

Smith AM, Stitt M (2007) Coordination of carbon supply and plant growth. Plant Cell Environ 30(9):1126–1149. https://doi.org/10.1111/j.1365-3040.2007.01708.x

Stein O, Granot D (2019) An overview of sucrose synthases in plants. Front Plant Sci 10:95. https://doi.org/10.3389/fpls.2019.00095

Takahashi Y, Tahara M, Yamada Y, Mitsudomi Y, Koga K (2018) Characterization of the polyamine biosynthetic pathways and salt stress response in *Brachypodium distachyon*. J Plant Growth Regul 37:625–634. https://doi.org/10.1007/s00344-017-9761-z

Veith R, Komor E (1993) Regulation of growth, sucrose storage and ion content in sugarcane cells, measured with suspension cells in continuous culture grown under nitrogen, phosphorus or carbon limitation. J Plant Phys 142(4):414–424. https://doi.org/10.1016/S0176-1617(11)81246-0

Waclawovsky AJ, Sato PM, Lembke CG, Moore PH, Souza GM (2010) Sugarcane for bioenergy production: an assessment of yield and regulation of sucrose content. Plant Biotechnol J 8(3):263–276. https://doi.org/10.1111/j.1467-7652.2009.00491.x

Wendler R, Veith R, Dancer J, Stitt M, Komor E (1991) Sucrose storage in cell suspension cultures of *Saccharum* sp. (sugarcane) is regulated by a cycle of synthesis and degradation. Planta 183(1): 31–39. https://doi.org/10.1007/BF00197564.

Winter G, Todd CD, Trovato M, Forlani G, Funck D (2015) Physiological implications of arginine metabolism in plants. Front Plant Sci 6:534. https://doi.org/10.3389/fpls.2015.00534

Xiong Y, Jiao Y (2019) The diverse roles of auxin in regulating leaf development. Plants 8(7):243. https://doi.org/10.3390/plants8070243

Xiong Y et al (2013) Glucose–TOR signaling reprograms the transcriptome and activates meristems. Nature 496(7444):181–186

Yuan Y, Xu X, Gong Z et al (2019) Auxin response factor 6A regulates photosynthesis, sugar accumulation, and fruit development in tomato. Hortic Res 6:85. https://doi.org/10.1038/s41438-019-0167-x

Zemlyanskaya EV, Omelyanchuk NA, Ubogoeva EV, Mironova VV (2018) Deciphering auxin-ethylene crosstalk at a systems level. Int J Mol Sci 19(12):4060. https://doi.org/10.3390/ijms19124060

Zhang M, Yuan B, Leng P (2009) The role of ABA in triggering ethylene biosynthesis and ripening of tomato fruit. J Exp Bot 60(6):1579–1588. https://doi.org/10.1093/jxb/erp026

Zhao Y, Chan Z, Gao J, Xing L, Cao M, Yu C, Hu Y, You J, Shi H, Zhu Y, Gong Y, Mu Z, Wang H, Deng X, Wang P, Bressan RA, Zhu JK (2016) ABA receptor PYL9 promotes drought resistance and leaf senescence. PNAS 113(7):1949–1954. https://doi.org/10.1073/pnas.1522840113