

Ten years of amino acid research at post-harvest: What is known so far? What comes next?

Abstract – Current information on the use of amino acids (AA) as a post-harvest treatment is barely over a decade old. In recent years, some alternative functions to protein structuring have been unravelled, and their possible mechanisms of action have been discussed up to date. Only 16 of the 20 protein AA have been studied, and, among these, some AA have been part of only one study. Therefore, the information to date remains somewhat limited. Listed here are the several important researches on the use of AA, at post-harvest, in whole or minimally processed fruits and vegetables. The effects of various AA derivatives, including much of the existing information on D-isomer amino acids (D-AA) were considered, highlighting the current legislation on the use of AA, taking into account the selection and use of high-purity AA over mixtures for application in the commercial chain, in addition to justifying their use over other frequently applied substances. This is the first known study to compile suggestions for the use of AA in commercial post-harvest stages.

Index terms: amino acid derivatives, amino acid isomers, commercial mixtures, current legislation, horticultural products, marketing chain.

Dez anos da pesquisa sobre aminoácidos na pós-colheita: O que se sabe até aqui? O que virá em seguida?

Resumo – As informações atuais sobre o uso de aminoácidos (AA) como tratamentos pós-colheita têm apenas pouco mais de uma década. Em anos recentes, algumas funções alternativas à estruturação de proteínas foram elucidadas, e seus possíveis mecanismos de ação têm sido discutidos até o presente. Somente 16 dos 20 AA em proteínas foram estudados, e, destes, alguns aminoácidos fizeram parte de apenas um estudo. Portanto, a informação atual permanece um tanto limitada. Estão listadas aqui inúmeras pesquisas importantes sobre o uso de AA, na pós-colheita, em frutos e vegetais inteiros ou minimamente processados. Os efeitos de vários derivados de aminoácidos foram considerados, incluindo-se muitas das informações sobre aminoácidos isômeros D (D-AA), tendo-se enfatizando a legislação atual quanto ao uso de AA, levando-se em conta a seleção e o uso de AA em condições de alta pureza ao invés de suas misturas para aplicação em cadeia comercial, tendo-se justificado o uso desses aminoácidos em lugar de outras substâncias frequentemente aplicadas. Este é o primeiro estudo conhecido a compilar sugestões para o uso de AA nos estágios de pós-colheita comercial.

Termos para indexação: derivados de aminoácidos, isômeros de aminoácidos, misturas comerciais, produtos hortícolas, legislação atual, cadeias comerciais.

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1. Introduction

Beyond being the constituents of proteins, amino acids (AA) may have more functions that are more specific. Not only these molecules are essential at a structural level, but also they can have antioxidant action, act against herbivores and pathogens, and mediate plant-pollinator interactions (Deng & Lu, 2017). The tolerance to abiotic stress in plants is also influenced by the induction of free AA as osmolytes. Proline is one of the most studied AA due to its various functions in vegetables derived from the action as an osmolyte or 'compatible solute'. It has the ability to scavenge reactive oxygen species, stimulates the activity of enzymes involved in oxidative metabolism, and it can also induce gene expression and buffer cellular redox potential (Szabados & Savouré, 2010; Tang et al., 2024). Ingrisano et al. (2023) manifest that both proline and cysteine are very important AA involved in the response to drought stress. Instead, Shim et al. (2023) found that osmotic stress causes branched-chain amino acid accumulation (leucine and valine) to increase many-fold. Alanine, phenylalanine, tryptophan, and methionine can serve as precursors for the synthesis of secondary metabolites such as glucosinolates (Kitainda & Jez, 2021; Pacheco-Sangerman et al., 2023), which are substances secreted as plant defense (Lv et al., 2022). Alanine is recognized as an osmolyte, just like proline and cysteine. Phenylalanine is the precursor to the metabolism of phenylpropanoids, which are extensively researched and found across the kingdom of plants. Since tryptophan produces indoleacetic acid, the precursor to auxins, it plays a role in the production of auxins (Mano & Nemoto, 2012). Methionine is one of the polyamine precursor molecules that act under low temperature stress conditions, as well as arginine (and lysine) (Sagar et al., 2021). Arginine is a precursor of lignans and hydroxycinnamic acid, and therefore has both a function as a signal and a structural molecule (Benstein et al., 2013). Amino acids with acidic groups (aspartic and glutamic acids) or basic groups (arginine, histidine, and lysine) can regulate cellular pH (Ninni et al., 1999). Some AA are associated with the growth and development of plant cells, since they can be involved in the rapid growth of meristematic tissues, as occurs with serine (Häusler et al., 2014). There are also AA that perform functions related to cellular energy balance. Significant alterations in AA metabolism are implied by the adaptation of plant metabolism to stress-induced energy deficiency (Heinemann &

Hildebrandt, 2021). The suppression of the anabolic processes occurs in tandem with the activation of pathways that utilize AA as substitute substrates. There is a relationship between the anti-browning action of a substance and its reducing power, as is the case of molecules that contain sulfhydryl groups, such as the AA cysteine and the tripeptide glutathione, which contains cysteine. The local synthesis of cysteine triggers the production of abscisic acid and, in addition, the degradation of cysteine produces the gas messenger hydrogen sulfide, which promotes the closure of the stomas by the persulfidation of proteins (Heinemann & Hildebrandt, 2021). There are numerous reports in which these substances have been effective in delaying enzymatic browning of whole and fresh-cut fruit and vegetable products (Gohari et al., 2021; Zhang et al., 2023a, 2023c). It is worth mentioning that there are also several studies with antibrowning action using AA arginine (Wills & Li, 2016; Prabasari et al., 2020) and, to a lesser extent, using aspartic acid, as reported in a single research work, (Feng et al., 2020). As we have observed, there are various functions of AA, beyond the basic function of giving structure to proteins. The present study aimed to emphasize the various roles of these natural substances, mainly in post-harvest of fruit and vegetables. Studies in which AA were used in post-harvest have been published almost entirely in the last decade (except for a work published in 2008). As expected, the results are biased in several AA and, for some of them – glutamine, histidine, valine, and threonine – there are no publications yet that display beneficial effects of AA in the post-harvest of horticultural products. To date, there is only one review linked to the use of AA in post-harvest fruit and vegetables, of very recent date (Yuxiao et al., 2023). The present study emphasizes the vast majority of existing works to date that have applied canonical proteinogenic L-amino acids in post-harvest (16 of the 20 AA), including their indirect mode of action as precursors of molecules with recognized functioning, information on D-amino acids, data about changes in the concentration of AA in the cell depending on different variables, information on the effects of various derivatives of AA in post-harvest (including nonprotein AA), knowledge on current legislation, and the feasibility of these substances being considered for application in the marketing chain, comparing the action of isolated AA against commercial mixtures or other best studied plant regulators.

1.1. Amino acid concentration in plants and vegetable produces

In plant cells under a normal state condition, the content of free AA is between 100 and 1000 times smaller than what is found in proteins; however, in plant cells under stress (an altered state), there is a higher content of free AA (Hildebrandt et al., 2015). Particular higher concentrations of various AA were found in *Arabidopsis* under different abiotic stress (Sun et al., 2010; Caldana et al., 2011; Obata & Fernie, 2012; Rao et al., 2013). Conversely to all previous researches, under starvation conditions *Arabidopsis* plants exhibited low amounts of glutamine, glutamate, aspartate, alanine, and methionine, indicating the inhibition of N and S assimilation (Osuna et al., 2007). Kaplan et al. (2004) realized that in both heat and cold shock, there were coordinated increases in the pool sizes of amino acids in *Arabidopsis*, produced from pyruvate and oxaloacetate and other suitable solutes, such as polyamine precursors. Furthermore, the authors found that there seemed to be a coordinated increase in a select group of amino acid derivatives with protective properties, namely GABA and β -alanine. This is in line with a study from several years ago on *Vigna unguiculata* (Mayer et al., 1990), and with a more recent research on lotus *Lotus japonicus* (Rocha et al., 2010). When cowpea (*Vigna unguiculata*) cells maintained at 26°C were transferred to 42°C, there was a rapid accumulation of GABA (>10-fold) while the quantities of total free amino acids raised by about 1.5 times, while in lotus under other stress condition, thus, water logging (anoxia), GABA, alanine and glutamate accumulates. In rice roots under high-chrome stress alanine, proline, and ornithine accumulates (Dubey et al., 2010). In a study developed on *Festuca trachyphylla*, Wang et al. (2018) found that varieties resistant to high-temperature stress (33-38 °C), compared to the control (18-21 °C), accumulated aspartate, glutamine, histidine, proline, threonine, and tryptophan. The varying levels of free AA under high-temperature stress was also observed for wheat grains (Hu et al., 2022). It is worth mentioning that few researchers have evaluated the influence of temperature in the amino acid content in vegetable produces. Strikingly, two separate studies – one on the plant and the other on the post-harvest stage – have been conducted on mandarins. In the pre-harvest study, it was found that, as the temperature rose throughout

the day, the overall amount of amino acids in the fruit tended to rise as well (Kim et al., 2021). The second study found that, varying temperatures in mandarin out of the plant, there was accumulation of ornithine and glutamine at 5 °C and, in a range of 20 to 30 °C, high concentrations of phenylalanine, tryptophan, valine, lysine, and histidine (Matsumoto & Ikoma, 2012). It should also be considered that the AA content in vegetables is usually modified when they experience biotic stress, for instance, in the fermentation process (Zhang et al., 2025). The effect of variation in endogenous AA levels in postharvest of horticultural products, under different stress conditions, especially of abiotic type, is a great niche for future research. Studies developed in the plant could serve as a tool to help better understand future postharvest studies.

1.2. Amino acid as precursors of important substances

In the animal kingdom, the catabolism of AA provides a series of nitrogenous substances that can lead to the biosynthesis of metabolites, such as neurotransmitters, melanin, creatine, thyroid hormones, carnitine, porphyrins and cholines. In the plant kingdom, amino acids are precursors of various molecules of vital importance for plant survival, among which are signaling molecules, compounds with antioxidant capacity, and substances that act against different types of stress or defense against predators (Table 1).

Some examples of important molecules synthetized by means of AA are purines and pyrimidines, glutathione (GSH/GSSG), polyamines, gamma aminobutyric acid (GABA), indoleacetic acid (IAA), nitric oxide (NO), glycine betaine (GB).

1.3. Amino acids and derivatives in post-harvest

1.3.1. Amino acids in post-harvest

A systematic search was conducted for scientific literature, using two search sites – Science Direct and Google Scholar –, to generate concise information on the role of AA in the post-harvest of fruit and vegetable products (Table 2). “Aminoacid + post-harvest” and “Aminoacid X + post-harvest” were the search words used, where “aminoacid X” denotes each of the twenty nonproteinogenic amino acids.

Table 1. Molecules with important functions synthesized from AA in plants.

AA (precursor)	Molecule(product)	Main functions	Source
Alanine	β -alanine Glucosinolates	Protection against biotic and abiotic stresses. Microbial and predator protection.	Parthasarathy et al. (2019) Lv et al. (2022)
Arginine	NO	Activity against ROS.	Hasanuzzaman et al. (2019)
	Polyamines	Regulate growth, development, and responses to biotic and abiotic stresses.	Roy et al. (2024)
Asparagine	(Other AA)	(<i>Indirect functions</i>)	-
Aspartate	(Other AA)	(<i>Indirect functions</i>)	-
Cysteine + Glutamate + Glycine	GSH/GSSG	Antioxidant activity. Osmoprotection.	Hasan et al. (2020)
Glutamate	Chlorophylls	Energy absorption. Nutrient generation.	Martins et al. (2023)
	GABA Ca^{2+} release (to cytosol)	Redox balance. Osmoprotection. Signaling for plant growth, development and defense responses	Ma et al. (2023) Verma et al. (2022)
Glutamine	(Other AA)	(<i>Indirect functions</i>)	-
Glycine	GB	Acts as a compatible solute.	-
Histidine	Histamine	Predator protection.	Akula & Mukherjee (2020)
Isoleucine	β -alanine Glucosinolates	(<i>See alanine</i>) (<i>See alanine</i>)	(<i>See alanine</i>) (<i>See alanine</i>)
Leucine	Glucosinolates	(<i>See alanine</i>)	(<i>See alanine</i>)
Lysine	(Other AA)	(<i>Indirect functions</i>)	-
Methionine	Ethylene	Ripening Senescence Abscission Epinasty	Binder (2020)
Phenylalanine	Polyamines Glucosinolates	(<i>See arginine</i>) (<i>See alanine</i>)	(<i>See arginine</i>) (<i>See alanine</i>)
	Phenolics	Structure Antioxidant activity Defense Signaling	Kumar et al. (2020)
Proline	Salicylic acid	Defense Growth and development	Kaya et al. (2023)
	ROS	Abiotic and biotic stress response	Hasan et al. (2020)
Serine	GABA	(<i>See glutamate</i>)	(<i>See glutamate</i>)
	GSH/NADPH	Redox balance	Ma et al. (2023)
Threonine Tryptophan	(Other AA) IAA	(<i>Indirect functions</i>) Cell growth, division and differentiation	- Hariprasad et al. (2021)
	Phytoalexins	Microbial protection	Ahmed & Kovinich (2021)
Tyrosine	Glucosinolates	(<i>See alanine</i>)	(<i>See alanine</i>)
	Alkaloids	Predator protection Precursor of secondary metabolites Growth regulation	Bhamhani et al. (2021)
Valine	Melatonin	Delays senescence Counteracts stress Antibrowning	Fan et al. (2023)
	Phenolics	(<i>See phenylalanine</i>)	(<i>See phenylalanine</i>)
Valine	Glucosinolates	(<i>See alanine</i>)	(<i>See alanine</i>)
	Glucosinolates	(<i>See alanine</i>)	(<i>See alanine</i>)

Abbreviations: NO, nitric oxide; GSH/GSSG, reduced and oxidized glutathione; GABA, gamma aminobutyric acid; GB, glycine betaine; ROS, reactive oxygen species; NADPH, nicotinamide adenine dinucleotide phosphate; IAA, indoleacetic acid.

Table 2. Application effect of amino acids on fruits and vegetables in the post-harvest.

Amino acid	Treatment	Outcomes	Source
L-Alanine	5 mmol L ⁻¹ ; immersion for 5 min	Inhibit post-harvest senescence of broccoli	Sohail et al. (2021c)
	50 mmol L ⁻¹ ; wound application	Antifungal effect against <i>Botrytis cinerea</i> in cherry tomato	Li et al. (2024)
	2 mmol L ⁻¹ ; immersion for 10 min	Less weight loss and polyphenol oxidase activity in okra pod	Fattahi et al. (2023)
	1 mmol L ⁻¹ ; immersion for 10 min	Maintain persimmon quality	Khan et al. (2023)
	1-5 mmol L ⁻¹ ; immersion for 15 min	Alleviate yellowing in broccoli	Malekzadeh et al. (2023)
	200 mmol L ⁻¹ ; immersion for 5 min	Delay enzymatic browning of fresh-cut pear and apple	Olgaç et al. (2023)
	1 mmol L ⁻¹ ; spraying	Enhanced antioxidant capacity in blueberry	Wang et al. (2023a)
	1 mmol L ⁻¹ (*)	Mitigates CI and maintains quality of Sandhuri guava fruit	Ali et al. (2022)
	5 mmol L ⁻¹ ; inside nanoparticles	Increased the chilling tolerance by reducing the accumulation of MDA and H ₂ O ₂ in plum	Mahmoudi et al. (2022)
	0.6 mmol L ⁻¹ Immersion, 10 min	Prolonged storage life in persimmon	Nasr et al. (2022)
	1 mmol L ⁻¹ ; immersion for 15 min	Maintained quality and nutraceutical properties of pomegranates	Shi et al. (2022)
	1-5 mmol L ⁻¹ ; wound application	Enhance the biocontrol efficiency of <i>M. citriensis</i> against <i>Geotrichum citri-aurantii</i> in citrus	Wang et al. (2022b)
	5 mmol L ⁻¹ ; immersion for 5 min	Inhibit post-harvest senescence of broccoli	Sohail et al. (2021a)
	2-100 mmol L ⁻¹ ; immersion for 5 min	Extended green life of leafy vegetables	Sohail et al. (2021b)
L-Arginine	0.05 mmol L ⁻¹ ; spraying	Delayed senescence in strawberry	Lv et al. (2020)
	50-150 mmol L ⁻¹ ; immersion for 5-15 min	Inhibit browning on fresh-cut <i>Salacca edulis</i>	Prabasari et al. (2020)
	1 mmol L ⁻¹ ; immersion for 2 min	Attenuates post-harvest decay and maintains quality of strawberry	Shu et al. (2020)
	0.5 - 2 mmol L ⁻¹ ; immersion for 15 min	Delayed CI in pomegranate	Babalar et al. (2018)
	0.05 mmol L ⁻¹ ; immersion during storage, (*)	Reduced disease incidence and losses of fresh weight and chlorophyll content in green asparagus	Wang et al. (2017)
	50-100 mmol L ⁻¹ ; immersion for 5-10 min	Delayed the development of browning, extending shelf-life in fresh cut Granny Smith apple, and doubled post-harvest time storage of iceberg lettuce	Wills & Li (2016)
	0.2 mmol L ⁻¹ ; ^a accum infiltration, 0.5 min	Amelioration of chilling stress in tomato	Zhang et al. (2013)
	5 mmol L ⁻¹ ; spraying	Promotion of stress resistance and wound healing in broccoli	Sun et al. (2023a)
	0.2 mmol L ⁻¹ ; immersion for 10 min	Resistance against <i>Alternaria</i> rot in jujube	Chang et al. (2022)
	50 mmol L ⁻¹ Immersion, 5 min	Inhibited browning in fresh-cut cabbage	Nilprapruk (2020)
(*) Asparagine	2 mmol L ⁻¹ ; immersion for 10 min	Reduced CI and weight loss by 37% in okra pod	Fattahi et al. (2023)
L-Aspartate	38-150 mmol L ⁻¹ ; immersion for 5 min	Delayed browning in potato	Feng et al. (2020)
	5 mmol L ⁻¹ ; immersion for 5 min	Inhibit post-harvest senescence of broccoli	Sohail et al. (2021c)
L-Cysteine	82.5 mmol L ⁻¹ ; immersion for 15 min	Less browning. Increased Cys, Glu, Ser and Leu level in cut apple pulp and peel	Zhang et al. (2023c)

Continue...

Table 2. Continuation.

Amino acid	Treatment	Outcomes	Source
L-Cysteine	0.412 mmol L ⁻¹ ; immersion for 10 min	Reduced weight loss, browning index, decay index, and respiratory intensity in loquat	Zhang et al. (2023a)
	0.825 mmol L ⁻¹ ; wound application	Higher resistance against <i>Monilinia fructicola</i> and higher antioxidant activity in plum	Wang et al. (2023b)
	8.25 mmol L ⁻¹ ; immersion for 10 min	Higher antioxidant activity in plum	Chen et al. (2022)
	33 mmol L ⁻¹ ; immersion for 15 min	Delayed internal browning and improve sensory quality in peach	Gohari et al. (2021)
	8.25 mmol L ⁻¹ ; immersion for 1 min	Prevent enzymatic browning in potato sticks	Cerit et al. (2020)
	0.8-4.0 mmol L ⁻¹ ; immersion for 10 min	Prevent enzymatic browning in plum	Sogvar et al. (2020)
	2-16 mmol L ⁻¹ ; immersion for 5 min	Enhances the content of betalains and polyphenols in fresh-cut red beet	Preczenhak et al. (2019)
	8.25 mmol L ⁻¹ ; fruit inoculation	Delayed <i>Monilinia fructicola</i> growth in plum	Yang et al. (2019)
	0.08-8.0 mmol L ⁻¹ ; immersion for 5 min	Delayed pericarp browning and suppression of lipid peroxidation in litchi	Ali et al. (2016)
	8.25 mmol L ⁻¹ ; immersion for 4 min	Delayed browning in fresh-cut lettuce	Pace et al. (2014)
L-/D-/DL- Cysteine	1-4 mmol L ⁻¹ ; immersion for 2 min	Prevent enzymatic browning in cherimoya	Campos-Vargas et al. (2008)
	5 mmol L ⁻¹ ; immersion for 5 min	Delayed senescence in broccoli and leafy vegetables	Sohail et al. (2021a, 2021b)
L-Glutamate	2-100 mmol L ⁻¹ ; immersion for 5 min	Extended green life of leafy vegetables	Sohail et al. (2021b)
	5x10 ⁴ mmol L ⁻¹ ; spraying	Delayed yellowing and senescence in pak-choy, parsley and mint	Al Ubeed et al. (2019)
	0.82-8.25 mmol L ⁻¹ Immersion, 5 min	Delayed senescence by improving the antioxidant capacity in goji	Wang et al. (2022a)
	(*) Immersion, (*)	Inhibited ethylene release and respiratory intensity to delay senescence of pear fruit	Jin et al. (2024)
	5.3 mmol L ⁻¹ ; immersion, (*)	Maintains quality and antioxidant capacity of fresh-cut carrot	Zhang et al. (2024)
	0.5 mmol L ⁻¹ ; immersion for 10 min	Maintains the quality of apple fruit	Li et al. (2023)
	34-103 mmol L ⁻¹ ; immersion for 4 min	Prevent the browning of fresh-cut potatoes	Song et al. (2023)
	0.7 mmol L ⁻¹ ; immersion for 15 min	Enhances resistance against <i>Botrytis cinerea</i> in tomato	Sun et al. (2019)
	0.7 mmol L ⁻¹ ; immersion for 15 min	Resistance against <i>Alternaria Alternata</i> in tomato	Yang et al. (2020a)
	0.01-10 mmol L ⁻¹ ; wound application	Resistance against <i>P. Expansum</i> in pear	Jin et al. (2019)
L-Glycine	5 mmol L ⁻¹ ; immersion for 5 min	Inhibit post-harvest senescence of broccoli	Sohail et al. (2021c)
	2 mmol L ⁻¹ ; immersion for 10 min	Diminished weight loss and CI in okra pod	Fattahi et al. (2023)
	5 mmol L ⁻¹ ; immersion for 5 min	Inhibit post-harvest senescence of broccoli	Sohail et al. (2021c)
L-Isoleucine	38-150 mmol L ⁻¹ ; immersion for 20 min	Delayed browning in potato chips	Meng et al. (2022)
	10 mmol L ⁻¹ ; in soaked filter paper	Promote anthocyanin accumulation in grape	Hattori et al. (2019)
L-Leucine	5 mmol L ⁻¹ (*)	Promoted the replication and repair of DNA, and delayed yellowing and oxidative damage in broccoli	Wang et al. (2024)
L-Lysine	0.1 mmol L ⁻¹ ; immersion for 10 min	Induction of <i>Alternaria</i> defense responses in pear	Liu et al. (2021)

Continue...

Table 2. Continuation.

Amino acid	Treatment	Outcomes	Source
L-Methionine	50 mmol L ⁻¹ ; wound application	Antifungal effect against <i>Botrytis cinerea</i> in cherry tomato	Li et al. (2024)
	5 mmol L ⁻¹ ; immersion for 5 min	Delayed senescence in broccoli	Sohail et al. (2021a)
	2-100 mmol L ⁻¹ ; immersion for 5 min	Extended green life of leafy vegetables	Sohail et al. (2021b)
(*) Methionine	0.67 mmol L ⁻¹ ; immersion for 10 min	Reduce the post-harvest decay of jujube	Liu et al. (2023)
	0.67 mmol L ⁻¹ ; immersion in PDA medium, (*)	Enhanced disease resistance against black spot rot jujube	Liu et al. (2022c)
	17 mmol L ⁻¹ ; immersion for 5 min	Delayed browning in litchi	Ali et al. (2018)
L-Phenylalanine	5 mmol L ⁻¹ ; immersion for 5 min	Inhibit post-harvest senescence of broccoli	Sohail et al. (2021c)
	0.1-10 mmol L ⁻¹ ; immersion for 5 min	Delayed CI in tomato	Aghdam et al. (2019)
L-Proline	43 mmol L ⁻¹ (*)	Less deterioration, less H ₂ O ₂ content, and higher activities of oxidative enzymes in cassava	Tang et al. (2024)
	90 mmol L ⁻¹ (*)		Liu et al. (2022b)
	15-20 mmol L ⁻¹ ; spraying	Delayed CI in citrus	Mohammadrezakhani et al. (2019)
	0.25-0.50 mmol L ⁻¹ ; immersion for 5 min	Reduced cold stress in grape	Mohammadrezakhani & Pakkish (2015)
L-Serine	5 mmol L ⁻¹ ; immersion for 5 min	Inhibit post-harvest senescence of broccoli	Sohail et al. (2021c)
L-Tryptophan	5 mmol L ⁻¹ ; immersion for 5 min	Inhibit post-harvest senescence of broccoli	Sohail et al. (2021c)
L-Tyrosine	5 mmol L ⁻¹ ; immersion for 5 min	Inhibit post-harvest senescence of broccoli	Sohail et al. (2021c)

*Nonavailable description. Abbreviations: CI, chilling injury; MDA, malondialdehyde; DNA, deoxyribonucleic acid. Nonincluded data: pre-harvest studies; post-harvest reports with adverse effects or with nonsignificant differences compared to the control; results in post-harvest of products that are usually associated with fruit or vegetables (example: mushrooms, flowers, etc.); research derived from combinations of amino acids with each other or with other substances in post-harvest. Cysteine is the only one of the 20 AA that have been used in postharvest from more than a decade. Only research from the last 10 years was included in the table.

Analysis of table 2

As seen in Figure 1, for only 10 years (since 2014), there has been an uninterrupted growing trend in the number of publications on the subject. The first record is from 2008. Although the number of studies is currently low (2024), it is expected that this one will rise to a value similar to that of 2023, or even exceed it.

Main bullets

- The first post-harvest study was conducted about a decade ago (2013).
- For 4 of the 20 proteinogenic AA, there are no scientific reports to date (glutamine, histidine, valine, and threonine).
- For 7 of the 16 AA studied, there is only one single published article.

- The concentrations ranged from 0.05 to 5x10⁴ mmol L⁻¹. Two thirds of the reports used concentrations \leq 5 mmol L⁻¹.
- Most of the studies do the treatment through immersion (1 to 15 min). Only a small fraction of the treatments has been done by spraying, wounding, or by means of embedded paper, films, or nanoparticles.
- The main effects of AA in post-harvest were the following: delay of senescence (about 25%), browning (20%), and microbial growth (15%); in addition to maintaining better quality (about 10%), less yellowing (about 10%), and less deterioration (about 10%).
- Studies on minimally processed vegetables barely reach 10% of the total.

The application of AA in post-harvest is distributed equally between fruit and vegetables and, within the

latter, the majority corresponds to inflorescences, while in fruit, a same fraction (20%), corresponds to drupe fruit (Figure 2).

Figure 3 attempts to represent the distribution of AA by function for the post-harvest studies carried out to date. 'Senescence delay' was the most addressed topic, followed by 'Antifungal action', 'Browning reduction' and 'Less chilling injury', respectively. With a variety of main effects, arginine has been, up to the moment, the most promising AA for postharvest use. This could be the result of being the AA that has been examined the most or that has shown the best outcomes. More distantly follows glutamate, cysteine, and then proline.

Effect of amino acids against fungi

Botrytis and *Alternaria* were the most studied fungi genera used to treat horticultural products with certain L-AA in post-harvest. This is consistent with the idea that one of the most significant post-harvest infections in fresh fruit and vegetables is through *Botrytis cinerea* (Hua et al., 2018). *Alternaria* is not far behind because it can induce post-harvest deterioration of numerous crops and causes spoilage in over 400 host plants as a plant pathogen (Tralamazza et al., 2018). *Monilinia* comes next as the genus of fungal pathogens that causes brown rot and generates big losses in the stone-fruit production worldwide.

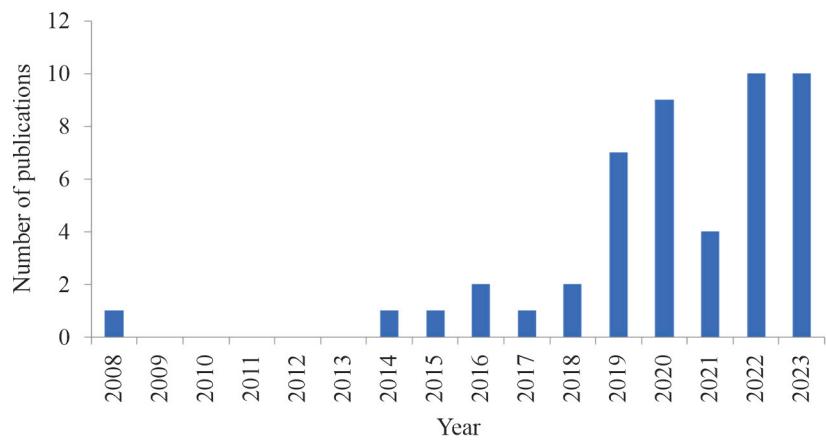


Figure 1. Number of published scientific works in which AA were used in fruit and vegetable products, by year.

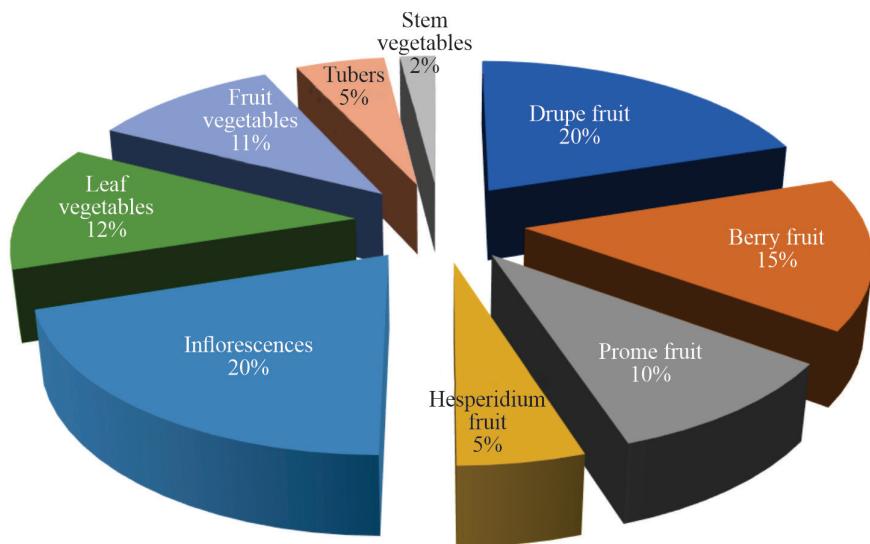


Figure 2. Percentage of studies in which AA were used in fruit and vegetable products, separated by category.

Effect of amino acids in fresh-cut products

All reports on fresh-cut fruit and vegetables have been effective in delaying or inhibiting browning, and most of them when treatments were done with arginine or cysteine.

D-amino acid occurrence in plants and post-harvest reports

An important biochemical characteristic of AA is their optical activity. Broad-spectrum racemases are the primary producer of D-amino acids (D-AA) from L-AA. All but glycine have one or two asymmetric atoms and can therefore exist in two optically active

(enantiomeric) forms (D and L) that have different physiological and biological activities. Naturally, the optic isomers of L-AA, the D-AA, are found in scarce amounts in plants. The quantity and variety of D-AA activities suggest that they are important to plant physiology (Kolukisaoglu, 2020). As D-AA were detected in gymnosperms, as well as in mono- and dicotyledonous angiosperms of the main plant families, it is concluded that free D-AA in a low percentage range are main constituents of plants (Zagón et al., 1994; Brückner & Westhauser, 2003). In many of them, as pea seedlings, tobacco leaves, wild rice, and lentils, D-Asp, D-Ala, D-Asn, D-Glu, D-Gln, and D-Ser are found naturally (Robinson, 1976). For a long time, it was believed that these molecules had an inhibitory

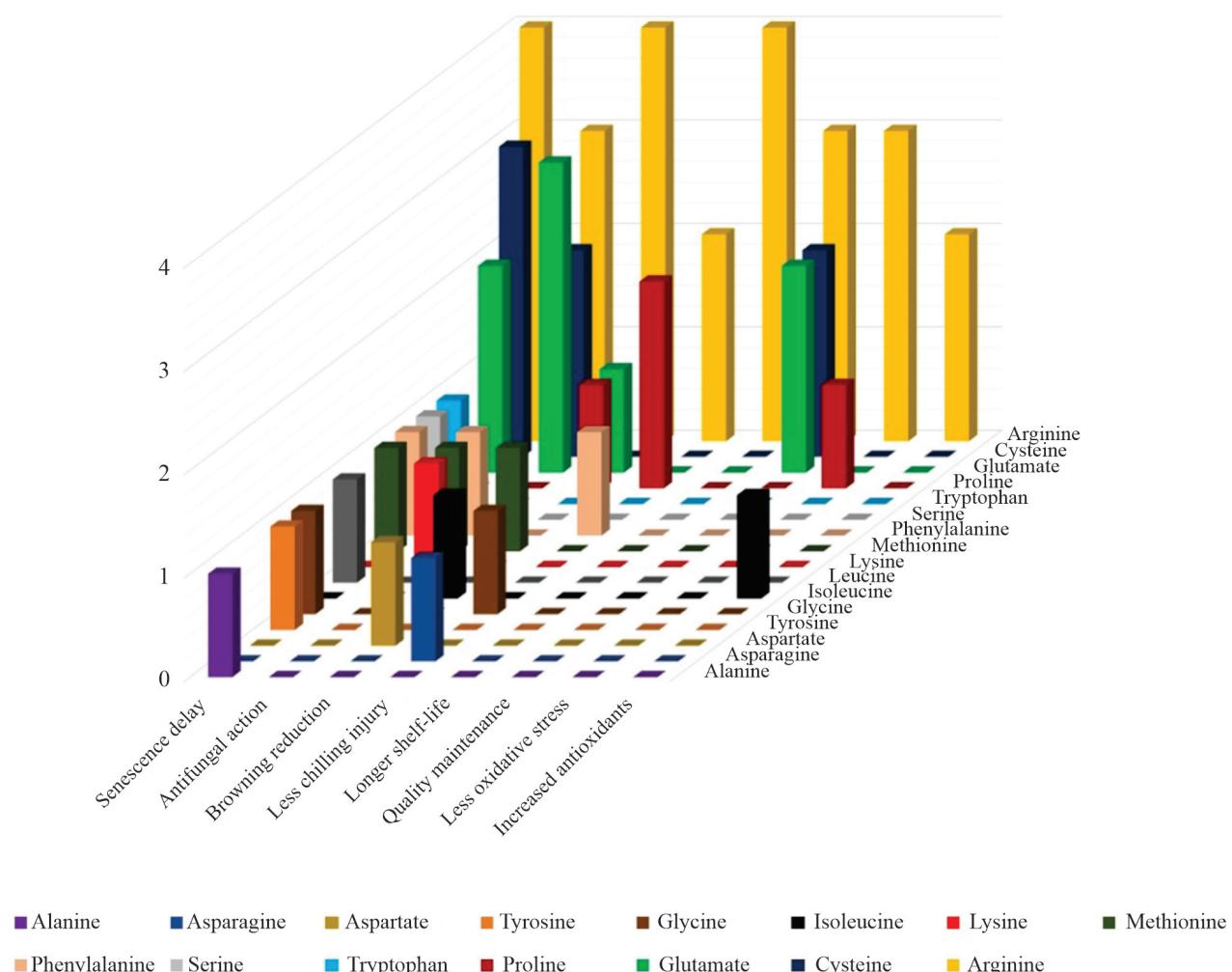


Figure 3. Relation between AA and their main effects in postharvest. The vertical axis indicates the number of publications to date that show a certain effect for a given AA. The alphabetical order of AA was altered to facilitate viewing.

or toxic effect in plants. However, as reported by Aliashkevich et al. (2018), this is a partial truth, since this depends on concentration, and alternatively, it has been found that these can play some important roles. The effect of some D-AA on plants, that is, in stages before harvest, has been thoroughly documented by these authors.

It is likely that D-amino acid metabolism enzymes, like racemases and transferases, fulfill important metabolic roles like serine, folate, or plastid peptidoglycan metabolism because they have been retained by higher plants and have not simply been eliminated, regardless of evolutionary steps, and it is possible that the metabolism of D-amino acids played a crucial role in maintaining the metabolic processes necessary for land plant evolution (Porras-Dominguez et al., 2024). The long-term suppression of plant growth caused by certain D-AA and their gradual decomposition has led to disregard their potential as crucial regulatory molecules. D-AA also can influence the chloroplast division and increase the synthesis of ethylene, or serve as a source of signaling molecules or nitrogen (Kolukisaoglu, 2020). Moreover, Kolukisaoglu & Suarez (2017) reported that plants can easily assimilate exogenous D-amino acids (D-AA) from the soil and generate a certain effect. For instance, D-Ile and D-Val increased the growth of *Arabidopsis* (Erikson et al., 2004). Besides, certain D-AA, such as D-His, D-Met, D-Phe, and D-Trp are converted between two and fifty times to their L-enantiomers (Suarez et al., 2019). These authors identified two explanations, one of which was the conversion of these D-AA to their respective L-enantiomers. The other was the increase in D-Glu and D-Ala concentrations after any particular D-AA treatment. In a previous work, the main molecule discovered was D-Ala, which was present at quantities more than 20 times greater than that of D-Glu (Kolukisaoglu & Suarez, 2017). Although D-Ala is one of the most toxic D-AA for *Arabidopsis* when administered exogenously, it appears to be the main product of D-AA metabolism in this species (Gördes et al., 2011). It was long believed that D-AA only inhibited plant growth, and consequently, plants developed defense systems to ward off and get rid of them. Conversely, new research indicates that plants can import and metabolize D-AA. The same processes that affect

D-AA may also be handled by transporters engaged in the uptake and transport of L-AA (Kolukisaoglu, & Suarez, 2017). The D-isomers of phenylalanine, valine, leucine, threonine, methionine, and ethionine significantly (up to 5-fold) increased the ethylene production from *Xanthium pensylvanicum* Wallr. seed, whereas the L-isomers had no such impact. In the seed tissues of *X. canadense* Mill., as well as in the cotyledonary segments from seed of *Helianthus annuus* L., *Cucurbita moschata* Duch., and *Vigna radiata* (L.) R. Wilczek, D-phenylalanine and D-methionine likewise induced the biosynthesis of ethylene (Satoh & Esashi, 1980). Derivatives of D-tryptophan may be precursors of the plant hormones auxin, as N-malonyl-D-tryptophan (MT) and D-tryptophan added to the medium, instead of auxin, stimulated the growth of soybean cell and tissue cultures and tomato (Rekoslavskaya, 1986). In fresh tea leaves (*Camellia sinensis*), a concentration increase of D-amino acids was found with the aging of the tea leaves, indicating that the enantiomerization of amino acids does not occur in biosynthetic processes (during the growth of the tea plants), but in post-harvest stages (Xu et al., 2020).

The effects of D-AA in post-harvest are very scarce. There is only one work (Table 2) in which the effect of an L-AA isomer (D-Cys) has been tested (Al Ubeed, 2019). Although there is only one other scientific work in post-harvest, using other D-AA (D-Arg), the results obtained were not what was sought, but in favor of ripening, since the synthesis of ethylene was induced (Wang et al., 2019).

1.3.2. Amino acid derivatives in post-harvest

Numerous aspects of plant growth and development, as well as biotic and abiotic stress responses, are regulated not only by AA, but also by some amino acid derivatives (Cai & Aharoni, 2022). Much of the existing information regarding the action of many AA derivatives in post-harvest has not been analyzed as a whole or systematized (Table 3). To make the table, a systematic search was conducted for scientific literature using two search sites (Science Direct and Google Scholar). “Aminoacid derivatives + post-harvest” and “Aminoacid derivative X + post-harvest” were used as search words, with “Aminoacid derivative X” denoting each of the molecules cited below.

Analysis of table 3

The concentrations used ranged from 0.003 to 2000 mmol L⁻¹, but more than 70% of the reports used concentrations \leq 50 mmol L⁻¹.

Immersion (1 to 15 min) was the method more used to provide the AA derivatives (as seen for AA). Only a small fraction of studies was treated by spraying, wound application, or using culture media.

The number of studies on fruit doubles that of vegetables.

Just over a third of the research were carried out on fruit vegetables and another third on tubers, the rest was distributed equally between leafy and inflorescence vegetables.

The main effects (in the percentage of studies) were the following: delay in microbial growth (about 45%), browning (about 15%), senescence (about 10%), and greater quality maintenance (about 10 %), associating the rest to more specific factors.

The studies carried out on minimally processed vegetables barely exceed 20% of the total.

Effect of amino acid derivatives against fungi

Botrytis cinerea has been one of the most studied fungus (as seen for AA), causing anthracnose together with *Colletotrichum* spp., and *Penicillium expansum*, responsible for blue mold. Unlike what has been observed for AA, studies have even been carried out with derivatives with positive effects against bacteria such as *E. coli*, among others (Abadias et al., 2011; Zhao et al., 2022). The antifungal action of e-PL is undisputed and is its most important effect in post-harvest.

Action of amino acid derivatives in fresh-cut products

Most studies developed on minimally processed horticultural products used cysteine derivatives, mostly N-acetyl-L-cysteine, an AA derivative that was effective against enzymatic browning and maintained overall quality.

Other amino acid derivatives used

Described below are the most important effects of a group of amino acid derivatives, which have a long scientific history to date.

Glycine betaine

Glycine betaine (GB) is a quaternary amine and an N-trimethyl derivative of glycine. This molecule is considered an osmotic adjuster that plays an important role in the stability and integrity of cell membranes. Glycine betaine plays an important role in overcoming environmental stress in plants through osmotic adjustment, carbon assimilation management, genetic regulation and cellular/subcellular protection (Ayub et al., 2022). It protects the structure of proteins and other macromolecules, thus improving the stabilization of enzymes and cold tolerance in horticultural crops. Among the mechanisms by which GB treatment in post-harvest can reduce CI are: the increasing of enzyme activity, such as catalase, ascorbate peroxidase, superoxide dismutase, or phenylalanine ammonia-lyase, decreasing the activity of polyphenol oxidase or peroxidase, limiting the accumulation of proline, and/or the delaying in the increase of oxidative metabolites as MDA or H₂O₂. By increasing the relative water content, the exogenous application of GB enhances plant tolerance to abiotic stress (such as drought, salinity, heat, cold, and/or heavy metals) and fosters plant growth, while shielding the plants from damaging substances. In other words, it keeps stable the plant cell's concentration of soluble carbohydrates, antioxidants, and osmolytes. To date, more than thirty research papers on GB post-harvest effects have been published so far, mainly in fruit (approximately 90%) and, to a lesser extent, in vegetables. The majority of beneficial effects (50% of the studies) were associated with the delay of chilling injury, followed by effects on overall quality (20% of the studies), and the rest on other post-harvest issues. The most commonly used concentration has been 15 mmol L⁻¹.

Glutathione

Glutathione is a tripeptide made up of the amino acids glutamate, cysteine, and glycine. Reduced glutathione (GSH) is a powerful antioxidant that is essential in the ascorbate-glutathione (AsA-GSH) pathway of plant cells, since it eliminates ROS and protects against oxidative damage (Zhou et al., 2023). In addition to promoting gene expression and enzymatic activity, GSH raises the levels of antioxidants and osmoprotectants such as soluble sugars, endogenous GSH, proteins, and polyamines. All this decreases

Table 3. Effect of the application of amino acid-derivatives in post-harvest products.

AA derivative	Treatment	Main results	Source
Hypotaurine	150 mmol L ⁻¹ (*)	Delays post-harvest softening of 'Kyoho' grape	Liu et al. (2022c)
	0.69 mmol L ⁻¹ ; immersion for 30 min	Delays senescence and maintain quality of peach fruit	Zhang et al. (2019)
N α -lauroyl-L-arginine ethyl ester (LAE)	2.4 mmol L ⁻¹ ; immersion for 10 min	Alleviates CI of cucumber	Hou et al. (2023)
	0.0832 mmol L ⁻¹ ; spraying	Inhibition of <i>Penicillium expansum</i> in citrus 'Benimadonna'	Cheng et al. (2022)
L-cysteine-hydrochloride	11.88 mmol L ⁻¹ ; immersion for 10 min	Reduction of <i>Escherichia coli</i> O157:H7 and <i>Listeria monocytogenes</i> counts and best quality in spinach	Zhao et al. (2022)
	0.003 mmol L ⁻¹ ; immersion for 5 min	Delayed senescence in longan	Li et al. (2018)
N-acetyl-L-cysteine	28.5 mmol L ⁻¹ ; immersion for 5 min	Inhibition of PPO (best at pH 7) in fresh-cut artichokes	Cabezas-Serrano et al. (2013)
	2000 mmol L ⁻¹ ; immersion for 2 min	Less cell wall degradation and abscission in grape	Yu et al. (2022)
γ -Poly-Glutamic Acid (γ -PGA)	122.6 mmol L ⁻¹ ; immersion for 1 min	Prevent enzymatic browning in potato sticks	Cerit et al. (2020)
	61.3 mmol L ⁻¹ ; immersion for 2 min	Reduced <i>E. coli</i> , <i>Salmonella</i> spp. and <i>Listeria</i> spp. counts in fresh-cut apple	Abadias et al. (2011)
N-acetyl-L-cysteine	25-45 mmol L ⁻¹ ; immersion for 5 min	Reduce browning, disease incidence and weight loss in longan	Sodchit et al. (2008)
	46 mmol L ⁻¹ ; immersion for 2 min	Reduce browning in fresh cut pear wedges	Oms-Oliu et al. (2006)
ϵ -Poly-L-lysine (ϵ -PL)	0.61 mmol L ⁻¹ ; immersion for 2 min	Higher quality maintenance in fresh cut potatoes	Cacace et al. (2007)
	(*); immersion for 3 min	Reduced browning in sliced apple	Son et al. (2001)
γ -Poly-Glutamic Acid (γ -PGA)	(*) (12.5-200 mg L ⁻¹); immersion for 1-10 min	Less decay and better preservation of 'Hongyan' strawberry	Shan et al. (2023)
	1-2 mmol L ⁻¹ ; immersion for 10 min	Resistance against <i>Phomopsis longanae</i> Chi in longan	Sun et al. (2023a)
ϵ -Poly-L-lysine (ϵ -PL)	(*)	Action against <i>Colletotrichum gloeosporioides</i> in jujube, fig, mango, tomato, apple and pitaya	Wu et al. (2023)
	2.3-5.3 mmol L ⁻¹ ; wound application	Defense against <i>Penicillium digitatum</i> mediated by fatty acids, in citrus	Zhang et al. (2023b)
ϵ -Poly-L-lysine (ϵ -PL)	6.7-13.3 mmol L ⁻¹ ; in PDA medium	Reduction of severity of damage by anthracnose in avocado	García et al. (2022)
	150-300 mmol L ⁻¹ ; wound application	Inhibition of <i>Penicillium expansum</i> in apples	Li et al. (2022)
ϵ -Poly-L-lysine (ϵ -PL)	2.5 mmol L ⁻¹ ; wound application	Effect against <i>P. expansum</i> in apple	Dou et al. (2021)
	48-94 mmol L ⁻¹ ; wound application	Effect against <i>Botrytis cinerea</i> in cherry, strawberry, grape, and pepper	Jiao et al. (2020)
ϵ -Poly-L-lysine (ϵ -PL)	333-666 mmol L ⁻¹ ; wound application	Action against <i>Botrytis cinerea</i> , through ROS in jujube	Li et al. (2019)
	300-600 mmol L ⁻¹ ; trapped in a film	Maintain quality for longer in chopped kiwi	Li et al. (2017)
L-Ornithine	(*); PDA medium (proportion 1: 9)	Effect against <i>P. digitatum</i> in citrus	Liu et al. (2017)
	5 mmol L ⁻¹ ; immersion for 5 min	Inhibit post-harvest senescence of broccoli	Sohail et al. (2021c)
Selenomethionine	306 mmol L ⁻¹ (*)	Improve sugar to acid ratio in strawberry	Gao et al. (2021)

*Nonavailable description. Synonyms: LAE, N α -lauroyl-L-arginine ethyl ester = Lauramide arginine ethyl ester = Lauric arginate; γ -PGA = γ -Poly-Glutamic Acid = Poly- γ -Glutamic Acid; ϵ -PL = ϵ -Poly-L-lysine = epsilon-poly-L-lysine hydrochloride = epsilon poly L-lysine HCl. Nonincluded data: results of the AA-derivatives most studied in previous years were not included in this table (like glycine betaine 'GB', glutathione 'GSH/GSSG', aminoethoxyvinyl glycine 'AVG' and gamma aminobutyric acid ('GABA')).

the generation of ROS and the accumulation of MDA and other harmful substances. Furthermore, GSH acts similarly to GB, since its exogenous application in plants increases water use efficiency, the level of osmoprotectors, and antioxidant enzymatic activity to combat salt stress (Khalid et al., 2022). To date, there are less than ten papers proving the effects of glutathione on post-harvest, all of them in fruit (only two in fruit vegetables), and its most important effect is distributed between the reduction of cold stress and the maintenance of quality. Postharvest GSH treatments have been performed more repeatedly with concentrations of 5 mmol L⁻¹.

Aminoethoxyvinyl glycine (AVG)

There are about forty-five post-harvest research works on the versatility of AVG to counteract different problems in post-harvest of horticultural products, especially in fruit. Only 10% of these studies have been developed in post-harvest of vegetables, limited only to tomato and cucumber, that is, only some fruit vegetables. Much remains to be known about the effect of AVG on this type of vegetables, and the field is clear for those of a different nature (leaf, inflorescence, stem, etc.). The most common exogenous AVG concentrations have been in the range of 0.25 to 1.5 mmol L⁻¹.

Aminobutyric acids

The 4-carbon nonprotein amino acid gamma aminobutyric acid (GABA) is found naturally in both plants and animals. Other isomers include beta-aminobutyric acid (BABA) and alpha-aminobutyric acid (AABA or homoalanine), which are naturally occurring in plants and have physiological roles in animals, respectively (Oketch-Rabah et al., 2021). Many fruits and vegetables naturally contain modest amounts of GABA, which accumulates under different abiotic stress situations and serves a variety of physiological purposes, including redox balancing, osmotic adjustment, and antioxidant activities (Signorelli et al., 2021; Arias Álvarez et al., 2022).

Alpha-aminobutyric acid (AABA)

To date, there is only one scientific work in which alpha-aminobutyric acid (AABA) has been used as a

post-harvest treatment, and in which no desired effects were observed, unlike what was observed using BABA and GABA (Fu et al., 2016). More studies should confirm the effect of AABA in post-harvest.

Beta-aminobutyric acid (BABA)

There are at least 25 studies using BABA in post-harvest. Seventy percent of the studies conducted have shown that the primary action of this substance is antibacterial. The other studies have focused on increasing the overall quality of fruit and vegetable products, preventing senescence, and abiotic stress. It has been used in the 90% of cases in fruit and only the rest 10% in vegetables. The most commonly used exogenous BABA levels ranged from 10 to 100 mmol L⁻¹.

Gamma aminobutyric acid (GABA)

The 4-carbon nonprotein GABA is found naturally in both plants and animals. It plays a physiological role in redox balance, osmoprotection, osmotic adjustment, and antioxidant activities, among other things. It is naturally present in modest amounts, in a wide variety of fruits and vegetables. It also accumulates under different abiotic stress conditions (Signorelli et al., 2021). Most plants have some protection against abiotic stress because of GABA (Sita & Kumar, 2020). This is because GABA increases antioxidant defense systems, which in turn improves plant stress tolerance. Additionally, there is a partial restoration of respiratory processes and energy production due to the stimulation of GABA production (Shelp et al., 2021). High-GABA concentrations increase the plant ability to withstand stress by enhancing photosynthesis, preventing the production of ROS, triggering antioxidant enzymes, and controlling stomatal opening during dry conditions (Kim & Yoon, 2023; Ru et al., 2024). There are fewer than 20 original articles that have used GABA as a post-harvest treatment. Most of them have shown an improvement in quality (around 50% of the studies), the rest have shown improvements in cold damage and in the activation of the plant defense system and, to a lesser extent, direct effects have been found in the regulation of ROS. As for glutathione, the most commonly used concentration was 5 mmol L⁻¹.

2. Current legislation for AA use

The regulation or legislation for the use of AA in agriculture, or potentially in post-harvest products, is linked to the pre-existing dispositions referring to the use of AA in human and animal foods.

2.1. Status among certifiers

While the majority of certifiers would forbid regular synthetic AA, certain regulatory bodies have determined that some of them are nonsynthetic and can be used as 'nonorganic' additives or as processing aids during post-harvest handling (USDA, 2007).

2.2. International Council on Amino Acid Science (ICAAS)

In response to the current worldwide efforts toward the establishment of dietary reference intakes for nutrients, the ICAAS has sponsored several international seminars on the assessment of sufficient intakes of AA. Following its official registration in 2008 as a nonprofit scientific association, the ICAAS quickly gained WHO/FAO Codex observer status. The establishment of the ICAAS in Tokyo, Japan, during the early 2000s was the result of an initiative by multiple AA production companies, to generate safety data regarding the use of proteinogenic AA in humans, and to ensure industry oversight of basic purity standards for amino acid-containing dietary supplements (Smriga, 2020). Recent studies on upper intake levels for leucine, L-thryptophan, methionine, arginine, L-lysine, histidine, serine, and ornithine were carried out at the request of the ICAAS (Elango, 2023).

2.3. European Food Safety Authority (EFSA)

Amino acids used in dietary supplements and PARNUTS (feedstuffs for particular nutrition purposes) products are now allowed in the EU, at background exposure levels that are typical for daily life. Nonetheless, research should be done to confirm the safety of AA, before companies can sell them at quantities that are significantly higher than those found in a typical diet (Roberts, 2016).

2.4. Food and Drug Administration (FDA)

The Food Chemicals Codex from the FDA (FDA, 2010) establishes that the following substances may be used safely in the food industry: the food additive consists of one or more of the following individual AA in the free, hydrated or anhydrous form or as the hydrochloride, sodium or potassium salts: L-Alanine, L-Arginine, L-Asparagine, L-Aspartic acid, L-Cysteine, L-Cysteine, L-Glutamic acid, L-Glutamine, Aminoacetic acid (glycine), L-Histidine, L-Isoleucine, L-Leucine, L-Lysine, DL-Methionine (not for infant foods), L-Methionine, L-Phenylalanine, L-Proline, L-Serine, L-Threonine, L-Tryptophan, L-Tyrosine, L-Valine.

The remaining amino acids are also considered safe for the food industry, but are listed in individual resolutions.

2.5. National Organic Standards Board (NOSB)

There are few and vague references to agroecosystem effects of AA in the literature. The majority rely on toxicological research conducted in laboratories. Since the use of AA as plant growth regulators is relatively recent, the long-term impacts of those substances have not been investigated. The majority of studies and data, which primarily focus on efficacy issues, come from entities with private interests. Most research and data, primarily regarding effectiveness concerns, originate from private firms. When used in compliance with good manufacturing practices, AA are classified by the FDA as "generally recognized as safe" (GRAS) and has no residue of heavy metals or other pollutants that exceed the limitations set by the FDA.

2.6. Environment impact: Historic use and EPA regulations

Since AA are 'natural', multiple certifying authorities have temporarily granted permissions for their use. According to the NOSB, AA disposal into the environment should not present a serious problem (NOSB, 2007). The US Environmental Protection Agency (EPA) is a regulatory body that is authorized by the US Congress to write regulations that explain the technical, operational, and legal details necessary to implement laws. It works to protect human health and the environment. For the use of AA, the EPA has detailed information specifically for each of them. On the EPA website (EPA, 2024), these substances

can be found one by one, by name or code (DTX code) and analyses of detailed information by categories and subcategories, such as: Hazard data (cancer, genotoxicity, etc.), exposure (product and use categories, toxics release inventory, exposure predictions, etc.), and literature (Google Scholar, Pubchem Articles, etc.).

3. Future perspectives

3.1 Potential challenges

Despite the ongoing research on postharvest proteinogenic AA, there is still much to explore. For several AA, their mechanisms of action have been proposed, as well as for some of its derivatives (Tables 4 and 5), but there are still others that remain undiscovered. Something similar occurs for the 20% of proteinogenic AA (glutamine, histidine, valine, and threonine) that are still absent in post-harvest studies. To this, few studies on the impact on fresh-cut products (apple, pear, salacca, cabbage, carrot, lettuce, and potato) and the scant data on D-AAs should be added, thus, only two research examples in post-harvest (using D-Cys and D-Arg). The effect of AA on minimally processed products is likely to be more limited in terms of success than on whole products, due to the number of functions to be fulfilled. Processing leads to multicausal deterioration, that is, oxidation, dehydration, enzymatic reactions, and growth of microorganisms, which limits the probability of success with respect to whole products. The chemical composition of the product and/or its internal structure affect it to a greater or lesser degree, and for this reason some of the treatments have achieved some advantage over a control. However, the disruption of cellular structures after processing releases nutrients to the surface, facilitating the growth of microorganisms that could also use some AA as raw material, before they exert their action on target tissues. The fact that D-AAs are generally more expensive than their L-isomers could be one of the reasons why they have not been investigated as much. Just as an increase in the number of studies using L-AA in post-harvest has been observed since 2019, the application of D-AA will likely be dragged towards a similar trend, although in a smaller number of studies in comparison.

3.2. Commercial brands vs pure AA

‘Amino acids are used in literally hundreds of combinations’ (NOSB, 2007). There are countless commercial brands of AA, and each one with specific formulations, that is, different combinations of AA with certain concentrations, and/or with excipients that makes each product unique. Furthermore, there could be synergistic or antagonistic effects between the different components. Although the commercial offer of AA mixtures is very wide, these are products applied to the field, where their use is mainly aimed at the growth and development of crops, that is, the use of AA as a base in the biosynthesis of proteins. Depending on the function sought, the crop or post-harvest product, the way the active ingredients is dissolved, and the form and moment of application, different results could be obtained. In other words, the consideration of these products with the purpose of post-harvest life extention and/or quality maintenance is far to be exploited because of the difficulty of evaluating the results. This leaves the door open to the consideration of the use of amino acid nature with high degree of purity.

3.3. Why use amino acids in post-harvest?

The use of AA could become more important in the future, not only because of its apparent GRAS characteristics, but also because of its cost. Despite being more expensive than their mixtures, AA, as high-purity active ingredients, it is still less expensive than several of the most well-known plant regulators that are currently in use, or may be in the future to provide some benefit in post-harvest. For instance, in the case of plant species susceptible to chilling, AA that functions as compatible solutes (such as proline, asparagine, etc.) could be employed as an alternative to polyamines (PA). On average, the cost of PA, considering more usual concentrations, as well as for the respective AA, is about 30 times higher on average. Alternatively, AA could be used to counteract biotic or abiotic stress instead of using abscisic acid (ABA) or brassinosteroids (BR). In this case, the relationship between cost and effective concentration for each substance is again in favor of AA, with a value 5 to 300 times lower, respectively. The above information was obtained systematically and in detail, searching for the cost for each of

Table 4. Mechanism of action of AA.

Aminoacid	Main functions and mechanism of action	Author
Alanine	Precursor of β -alanine, an osmoprotectant (compatible solute). These are low-molecular-weight substances that are released into the cell cytoplasm in response to different types of abiotic stress. Their uniqueness makes them difficult to metabolize, and they do not intervene in other cellular processes. These compounds are osmoprotective, since they stabilize the differences in osmotic pressure between the cellular environment and the cytosol.	Khalid et al. (2022) Parthasarathy et al. (2019) Kumar et al. (2018) Wani et al. (2013); Iba (2002)
Arginine	Precursor of PAs and nitric oxide, which are important regulators of biotic and abiotic stress responses and developmental processes that have the ability to capture free radicals. Polyamines also induce a general retention of antioxidant levels. Specifically, the ascorbate peroxidase, catalase, monodehydroascorbate reductase, dehydroascorbate reductase, and superoxide dismutase are examples of AOX enzyme activities that PAs have likely up-regulated, showing strong AOX capability.	Mishra et al. (2022) Winter et al. (2015)
Asparagine	Osmoprotectant. (For more details, see “Alanine”.) Asparagine also plays a primary role in nitrogen recycling, storage, and transport in vegetative and senescence organs.	Guo et al. (2023) Gaufichon et al. (2016)
Aspartate	Antibrowning action due to PPO inhibition, by reducing pH and chelating Cu^{2+} .	Feng et al. (2020)
Cysteine	Contains a sulfur donor group that is used in defense against oxidative stress and vital biomolecule synthesis. Cys and its derivatives are involved in the redox signaling of events that take place in different cellular compartments. The thiol/sulphydryl group (-SH), such as in Cys derivatives (GSH and NAC), makes these molecules effective enzymatic browning inhibitors, by means of two distinct mechanisms: 1) direct PPO inhibition, due to the -SH group's affinity for the copper ion at the enzyme's active site, resulting in physicochemical changes, which lead to its deactivation; 2) interaction of Cys with quinone intermediates to create stable colorless products.	Romero et al. (2014) Cerit et al. (2020)
Glutamate	Controls the defense responses, growth, and development in plants. Precursor of GSH, involved in redox balance. Precursor of GABA, which is crucial for maintaining the equilibrium of multiple cellular activities, as well as the metabolism of carbon and nitrogen. Precursor of IAA – the primary auxin to which Glu can conjugate –; is headed for oxidative destruction, when it combines with IAA-Glu. Precursor of salicylic acid, a stress defense inducer.	Liao et al. (2022)
Glycine	Glycine betaine precursor, an osmoprotectant. (For more details, see “Alanine”.)	Giri (2011)
Isoleucine	Precursor of β -alanine. (For more details, see “Alanine”.)	Rouhier et al. (2019)
Leucine	Promotes mRNA recycling, alleviating energy deficiencies. Improves nitrogen metabolism efficiency and attenuates oxidative damage via a decrease in ROS and the regulation of the antioxidant and osmotic systems.	Wang et al. (2024) Sun et al. (2022)
Lysine	Conversion to glutamate and other stress-related metabolites, in response to stress and in specific developmental programs.	Arruda & Barreto (2020)
Methionine	Methionine and S-adenosylmethionine are involved in the biosynthesis of polyamines, which responses to biotic and abiotic stresses. (For more details, see “Arginine”.)	Yang et al. (2020b)
Phenylalanine	One of the few characteristics known to be linked to the mode of action of Phe is that it is located upstream of several growth hormones and secondary metabolites, presenting a variety of biological roles and attributes, including defense against biotic and abiotic stress.	Tzin & Galili (2010)
Proline	Osmoprotectant. Pro acts as a signaling molecule to recover from stress situations, modifying mitochondrial processes, triggering specific gene expression and promoting cell death or proliferation. (For more details, see “Alanine”.)	Dikilitas et al. (2020) Szabados et al. (2010)
Serine	Precursor of Gly, Met, and auxins, which may delay senescence. Fundamental role in metabolism and signaling.	Ros et al. (2014)
Tryptophan	Precursor of melatonin, hormone that delays senescence and acts against different stress situations and quality degradation. The induction, interaction, and coordination of melatonin with reactive oxygen species, many plant hormones, and other signaling molecules are responsible of its numerous biological functions in postharvest. These processes improve antioxidant and defense systems, lessen oxidative damage, and preserve energy.	Aghdam et al. (2023) Ze et al. (2021) Xu et al. (2019)
Tyrosine	Precursor of a wide range of specialized metabolites with a variety of physiological functions, including defense chemicals and nonprotein amino acids. (Limited research).	Schenck & Maeda (2018)

Table 5. Mechanism of action of AA derivatives.

AA derivative	Main functions and mechanism of action	Author
Hypotaurine	Hydroxyl radical scavenger. Stimulator of antioxidant defense systems and H ₂ O ₂ . Induces enzymatic antioxidant capacity and its gene expression.	Liu et al. (2022c) Zhang et al. (2019)
Na-lauroyl-L-arginine ethyl ester (LAE)	LAE is a cationic surfactant. Strong activity against both gram-positive and gram-negative bacteria, yeasts, and molds.	Nerin et al. (2016) Asker et al. (2009)
L-cysteine-hydrochloride	(See "Cysteine").	Romero et al. (2014) Cerit et al. (2020)
N-acetyl-L-cysteine	(See "Cysteine").	Romero et al. (2014) Cerit et al. (2020)
γ-Poly-glutamic acid (γ-PGA)	Enhances antioxidant system capacity. (Very limited research).	Shan et al. (2023)
ε-Poly-L-lysine (ε-PL)	-Effect on gram-negative bacteria. ε-PL interferes with cell membranes through cationic polypeptide and negatively charged cell surface interaction via ionic adsorption. This reaction is thought to involve stripping the lipopolysaccharide layer, which permeabilizes the outer membrane. ε-PL competes with divalent cations for binding to phosphate groups in the inner core of LPS, and it causes shedding from the outer membrane of gram-negative bacteria. -Effect on mold. ε-PL induces membrane damage, thus causing increased extracellular conductivity and MDA accumulation, possibly as a result of the treatment's release of ROS. As the composition of fatty acids in the membrane is affected, this acquires curvature that alter its physico-chemical properties, causing the fungal cells to undergo apoptosis. Like in gram-negative bacteria, ε-PL may target some molds, due to the negatively charged membrane surface (<i>B. cinerea</i> , <i>S. cerevisiae</i> , <i>Alternaria alternata</i> , <i>Candida albicans</i>). In addition, ε-PL increases the expression of genes connected to the host's pathogenesis-resistance pathways. Finally, ε-PL at high concentrations can induce an efflux of K ⁺ and Ca ²⁺ and, thus, an efflux of material as short peptides and phosphate, causing a decrease in cell viability.	Vaara (1992) Shima (1984) Hyldgaard et al. (2014) Padilla-Garfias (2022) Shu et al. (2021) Jiao et al. (2020) Bo et al. (2014)
L-Ornithine	Precursor of proline. (For more details, see Proline.)	Rocha et al. (2012)
Selenomethionine	Selenium is a trace mineral with potent antioxidant effects, and selenomethionine has been found to be the safer, more bioactive form. (Very limited research.)	Gao et al. (2021)

those substances on the Sigma-Aldrich website, and it was related to a fixed volume of product (one liter) with the most effective concentration used for each of them. Specifically, each of the 20 AA were analyzed one by one in detail, as follows: four of the most well-known PA (cadaverine, putrescine, spermidine, and spermine); the two most commonly used BR (24-epibrassinolide and brassinolide); and abscisic acid.

4. Conclusions

The present review conglomerates much of the information that exists to date, regarding the use of AA and many derivatives in post-harvest of horticultural products. In one hand, data regarding the existence of D-AA and its main functions have been concentrated. On the other hand, knowledge about the laws under which these molecules are framed, depending on different regulatory entities

has been provided. Furthermore, the preference to use AA alone, instead of using some other hormonal regulators or combinations of AA, has been questioned. There is a lack of key information that should be found out on this topic; therefore, it is necessary to work more, to reliably assert some of the premises obtained by different researchers. It is worth mentioning that even less is known about AA derivatives; there is an innumerable quantity of these substances, for which their post-harvest effects are unknown, or for which their regulation of use does not exist yet or is not clear (for each molecule a systematic search was carried out). This information emerged from an exhaustive search with more than 60 examples. Finally, there are some questions that do not yet have solid answers in this field of study. Will some of these substances be able to meet market requirements? Will they accomplish it profitably and safely? Will this alternative have global reach or can it only be exploited by some sector?

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Uninformed: use of data not informed; research data was not used.

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No generative artificial intelligence (AI) was used in this study.

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The authors declare no conflicts of interest.

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